Using citizen science data to reveal the role of ecological processes in range changes of grasshoppers and crickets in Britain

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Abstract

Climatic and land use changes are affecting the distributions of many species and habitats. A detailed understanding of these impacts is critical for conservation and adaptation planning, but much interspecific variability remains unexplained. One reason may be that studies have tended to consider only effects of changes in mean climate, not of annual variation. Using data of the Orthoptera Recording Scheme and additional field observations, I investigated effects of species traits and seasonal variability in weather on the pattern and process of distributional changes of grasshoppers and crickets in Britain over recent decades. I found large changes in the distributions of several species, and relatively greater increases for habitat generalists, species that oviposit in vegetation, and for those with a southerly distribution. In a study of the rapid range expansion of two wing-dimorphic species, *Conocephalus discolor* and *Metrioptera roeselii*, I found some of the first evidence for effects of seasonal weather on annual colonisation rates, and for an interaction between the effects of temperature and precipitation. The findings suggest that for some species weather may concentrate dispersal into waves in climatically favourable years. This may increase successful establishment through greater numbers of colonists, and may also be advantageous in fragmented landscapes, allowing species to invest in dispersal only sporadically and under favourable conditions. The results also highlight the importance of considering interactive effects of temperature and precipitation when examining species' responses to climatic variability. Studies like these are made possible by large-scale, long-term distribution recording by volunteers. However, the unstructured and evolving nature of this "citizen science" makes the data prone to biases that need to be taken into account during analysis. I reviewed current recording of Orthoptera and the scope for its development, and propose a protocol for Orthoptera abundance monitoring by volunteers for future research and conservation applications.

List of Contents

List of Figures

List of Tables

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Author's declaration

I declare that this thesis is a presentation of original work and I am the sole author, except where appropriate acknowledgement is given. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as references.

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1. Introduction

Changes in the distributions of species and their habitats are one of the most fundamental and important changes occurring in the natural world in response to current alterations in climate and land use. These changes are likely to continue throughout this century and beyond. A detailed understanding of the pattern of these distributional changes and the underlying processes is critical for conservation and adaptation planning. While broad patterns of species' responses have been documented, a great deal of variability between and within species remains unexplained. As ectothermic insects of open habitats, grasshoppers and crickets (Orthoptera) are sensitive to the effects of climatic and land use changes. The Orthopteran species in Britain have a range of biological and ecological traits, and include several wing-dimorphic species, making dispersive individuals easily identified in the field. These characteristics make the group particularly suitable for investigation of range change processes, and of variation in responses to environmental change. Britain has a strong tradition of biological recording by naturalists, with recording schemes for many species groups, including Orthoptera, that have been active for decades. Such biological recording that relies on contributions from volunteer recorders, now often referred to as "citizen science", has allowed monitoring of species distributions over temporal and spatial scales that would be unachievable otherwise. However, the unstructured and changing nature of this type of data collection makes the records prone to various biases that need to be taken into account during analyses. Using data of the Orthoptera Recording Scheme and additional field observations, this thesis investigates inter- and intraspecific variability in responses to climatic and land use change of Orthoptera in Britain over recent decades, and some of the underlying ecological processes. It also evaluates current recording of Orthoptera and the scope for its development for future research and conservation applications.

1.1 Species ranges and range changes: introduction, definition and importance

This section introduces and defines the concepts of species distributions and distributional changes for the purposes of this thesis, and introduces the main factors and processes limiting distributions and driving distributional changes. The main current drivers of distributional change, and ways in which their effects have been investigated so far, including through the use of citizen science data, are then discussed in greater detail in subsequent sections in order to set out the approach and questions tackled in this thesis.

1.1.1 Ranges and range changes

The range or distribution of a non-migratory species can be defined as the area in which it has breeding populations. This area can be described either in terms of the species' "extent of occurrence", i.e. the area inside the smallest continuous convex boundary that can be drawn around all populations; or in terms of its "area of occupancy", i.e. the area within this extent of occurrence which the species actually occupies (IUCN 2012). The size of the area of occupancy depends on the spatial resolution at which it is mapped. Unless otherwise specified, in this thesis a species' distribution or range is taken to mean its area of occupancy in Britain at a 10km grid square resolution, which is the standard resolution of national distribution maps.

Alongside the origins of the diversity of species on Earth, the reasons underpinning the different distributions of species have intrigued biologists since the time of Charles Darwin and Alfred Russell Wallace. The main parameters determining the extent and location of a species' global distribution are: abiotic factors such as climate and geology, with a species' physiological limits determining the range of conditions in which it can reproduce; biotic factors such as food sources, competitors, predators and pathogens; its dispersal ability, colonisation history and geographical barriers to dispersal such as oceans, deserts or mountain chains; and genetic factors, such as gene flow from central populations limiting adaptation to environments beyond the current distribution (Brown and Lomolino 1998, Gaston 2003). Changes in any of these "biogeographic" parameters determining species' ranges can lead to distributional changes: range expansions through colonisations of new areas, or range contractions through local extinctions.

Species' ranges and range changes are therefore important parameters that indicate species' environmental and ecological tolerances and their past and present fortunes. They are fundamental measures of species' conservation status, and distribution size and trend are used as key criteria in assessments of extinction threat (Mace et al. 2008). Changes in one species' range will often affect others: interspecific differences in range changes lead to changing community compositions, and may therefore have important ecological consequences (Schweiger et al. 2008, Gilman et al. 2010, Le Galliard et al. 2012). Similarly, where species play important ecological and ecosystem service roles, changes in their distributions may indicate the degree of resilience of these systems to environmental change (Oliver et al. 2015a).

1.1.2 Range margins

Range margins can be defined as the geographical edges of permanently occupied species distributions (Gaston 2003). In this thesis, range margins are taken to mean the 10km grid squares at the furthest extent of a species' area of occupancy in any given direction, e.g. the northern range margin refers to the squares with the highest latitude (Hickling et al. 2006). The factors limiting the extent of species' distributions and the processes involved in range expansion and contraction through colonisation and extinction may come into focus towards the range margins, where species are often restricted to a narrower range of habitats than in the range core that provide optimal conditions (Thomas et al. 1986, Oliver et al. 2009). While species distributions are usually not continuous in the range core either, the degree of fragmentation of suitable habitat is consequently likely to be greater towards the range margins (Hanski 1999, Gaston 2003). Studies of species in regions near their range margins may therefore be particularly suitable for understanding their ecological requirements, and the factors and processes driving or limiting range changes, such as environmental change, availability and spatial arrangement of suitable habitat, and species' dispersal ability and dispersal processes (Hill et al. 2001, Gardiner 2009).

Species' distributions are therefore determined by a range of factors, whose influence may be particularly apparent near the range margins. Any change in these factors over time may drive distributional changes in species, which in turn may first become apparent at the range margins. The following section sets out the most important current drivers of distributional changes in order to illustrate their pervasive and rapid nature and provide context for the subsequent review of studies of their effects on species to date.

1.2 Drivers of distribution change

1.2.1 Historical vs. present drivers

Historically, important drivers of distributional changes of species have included changes in climate, evolution, natural dispersal of species, and geological processes. More recently, human activity has become the dominant factor affecting many species and regions, through land use change, anthropogenic climate change, pollution, overexploitation, and anthropogenic movement of species (Millennium Ecosystem Assessment 2005a). Human influence is now so pervasive that the term "Anthropocene" has been proposed to describe this epoch of significant human impact on the natural world (Crutzen 2002). In Britain, the principal factors affecting many taxonomic groups over recent decades have been land use and anthropogenic climate change, and they are likely to continue to be important for the next decades and beyond (Burns et al. 2016, Hayhow et al. 2016). These two drivers are discussed in the following sections, including pollution in so far as it is associated with land use.

1.2.2 Anthropogenic climate change

Global average surface air temperatures have risen by about 1.0°C since the late 19th century, largely caused by human activities that have increased levels of greenhouse gases such as CO_2 and methane in the Earth's atmosphere (Wolff et al. 2014). Much of this temperature rise has occurred in the past 30 to 40 years, with 16 of the 17 warmest years globally observed since 2001, making the speed of recent warming faster than most past climatic changes (Wolff et al. 2014, NASA 2017). Further warming of 2.4-4.6°C is expected globally by the end of the century if greenhouse gas emissions continue to rise unchecked; if emissions are reduced in line with current "Intended Nationally Determined Contributions" under the Paris Agreement, temperatures are projected to rise by a further 1.6-2.1°C over current levels, although the agreement aspires to limit warming to 1.5-2.0°C over pre-industrial levels, i.e. only 0.5-1.0°C of further warming (Wolff et al. 2014, Rogelj et al. 2016).

Changes in precipitation have also been observed and are expected to continue, for example increases in rainfall in northern temperate regions (UK Met Office 2015). Rises in temperature will also affect river flows and availability of water, and droughts are projected to increase in frequency in regions like the Mediterranean, southern Africa and south-east Asia (UK Met Office 2013).

Climatic changes are occurring unevenly across the globe, with greater warming over land surfaces than over the sea, and greater warming in northern regions than at lower latitudes (Wolff et al. 2014). Changes may also vary by season, for example in Britain spring temperatures have increased more than for other seasons, and winter precipitation is projected to increase by 10-30% by the 2080s, but summer precipitation to decrease by a similar amount (Parker et al. 1992, Murphy et al. 2009). Altogether this means that some regions and seasons are experiencing considerably greater, and others lower, than average climatic changes. Annual variability in weather is also predicted to increase, with more frequent and greater extremes, and with a potential for more severe weather events such as heavy rain storms (Wolff et al. 2014, UK Met Office 2015).

1.2.3 Anthropogenic land use change and pollution

Conversion of natural habitats for food production and other land uses has been one of the paramount anthropogenic influences on the natural world. Transformation of natural habitats for agriculture reached its highest rates globally in the second half of the 20th century and continues in many developing countries (Millennium Ecosystem Assessment 2005a). In contrast, in developed countries conversion of habitats for farming has tended to slow or stabilise. In Europe, farming subsidies led to very large areas of land being taken out of production as “set-aside” from 1990 onwards. In England set-aside soon exceeded 10% of arable land, equating to several hundred thousand hectares, and remained at this level until payments for set-aside were stopped from 2008 (Defra 2016). Forest cover in temperate regions of Europe, North America and Asia has increased over recent decades, including through abandonment of marginal agricultural land, while it has continued to decline in tropical regions (Hansen et al. 2013, FAO 2016).

Short of conversion of habitats, land use change may also affect habitat quality, for example through nutrient enrichment or cessation of traditional management. Modern intensive farming methods are characterised by high inputs of fertilisers and pesticides, and on many intensively used grasslands, monocultures of very few grass species with frequent cuts for silage instead of fewer cuts for hay. Nitrogen fixation through human activity, mainly fertilizer production, now equals or exceeds fixation in natural ecosystems, and despite some advances in precision application, considerable proportions continue to be lost to the environment (Robinson and Sutherland 2002, Millennium Ecosystem Assessment 2005b). Large areas of the UK exceed “critical loads” of nutrient nitrogen, i.e. levels harmful to sensitive elements of the environment (Stevens et al. 2011). In Britain, vegetation in many habitats has become less diverse, taller, and more shaded between 1978 and 2007, with light-loving species of shorter turf declining, and competitive species characteristic of fertile ground increasing (Carey et al. 2008). Pesticides (insecticides, herbicides, fungicides) have contributed to a dramatic increase in crop yields from the middle of the 20th century, but have also reduced the diversity of plants, invertebrates and other species of the farmed landscape and beyond (Carson 1962, Woodcock et al. 2016).

There are efforts in many countries to reduce the impacts of food production on the natural world, which have had variable success. Some of the most harmful and persistent pesticides have been phased out successfully, with organochlorines such as DDT banned in many industrialised countries in the 1970s, and world-wide in 2001 (UNEP 2017). However, applications of chemicals keep creating new environmental challenges and novel impacts on non-target organisms, such as the catastrophic effects of veterinary use of Diclofenac on Asian vulture populations (Oaks et al. 2004), and sub-lethal effects of neonicotinoid pesticides on wild bees (Whitehorn et al. 2012, Woodcock et al. 2016). In Britain the amounts of pesticides applied to farmland have decreased, but the number of pesticides used continues to increase (Robinson and Sutherland 2002). Organic farming practices have seen a revival in many industrialised countries, currently accounting for about 3% of agricultural land in the UK (Defra 2015). Organic farming has benefits for local biodiversity (Fuller et al. 2005), but organic yields are typically 25% lower than conventional yields, meaning that larger areas of farmland are required for the same output, although this varies by crop and site (Seufert et al. 2012). In the European Union, agri-environment schemes (AES) aim to support wildlife on conventional intensive farmland. Well-designed AES can have biodiversity benefits and do not necessarily affect yields negatively – they can even increase them for some crops (Pywell et al. 2015).

Anthropogenic changes in climate, land use, and land use intensity are pervasive in many habitats and regions. Separately or in combination, these drivers may significantly affect the populations and distributions of many species – positively or negatively – with potential implications for conservation, community compositions, and ecosystem functioning. Such impacts, and the ways in which they have been investigated, are the subject of the following sections.

1.3 Suitability and importance of insects as study systems

Regional investigations of exemplar taxonomic groups which share broad attributes and the way in which they are recorded and monitored, have proved a fruitful and practicable approach to studying impacts of large-scale environmental changes. Ideally, species groups investigated should be sensitive to the changes in question, amenable to sampling and observation, and of wide ecological and economic importance. This section assesses the suitability of insects (particularly Orthoptera) as study systems, and their ecological and economic importance.

1.3.1 Suitability as study systems

Insects have a number of traits which make them highly sensitive, and able to respond rapidly, to climatic and land use changes: they are ectothermic organisms, i.e. they largely rely on environmental heat sources to regulate their body temperature; many species occupy narrow ecological niches with specific requirements including vegetation structure; many insects have short generation times and large numbers of potential offspring; and many insects can fly or have other effective means of dispersal (Gullan and Cranston 1994, Thomas and Clarke 2004, Thomas et al. 2004b). While these traits mean that insect populations are likely to respond to environmental changes more rapidly than other species, they may also fluctuate considerably due to other factors such as interactions with predators and parasitoids (Gullan and Cranston 1994). Assessments of responses to environmental changes therefore need to be made at suitable scales, for example trends in population abundances need to be averaged over several years where the aim is to assess overall population trajectories (Fox et al. 2015).

Insects are by far the most diverse group of animals on Earth, constituting more than half of all known species (Chapman 2009). This means that comparative studies can investigate the different responses of species within one insect group, which have a variety of life histories and ecologies, such as different generation lengths, degrees of resource specialism, or dispersal abilities, while still being similar enough to be comparable (Angert et al. 2011). At the same time however, their species richness means that for many insect groups, monitoring data is limited in its coverage and scale in many regions, and studies have therefore tended to focus on a small number of taxa with the best data (Thomas 2005).

As ectothermic species of predominantly open habitats, grasshoppers and crickets are very responsive to climatic and land use changes (Willott and Hassall 1998, Simmons and Thomas 2004, Gardiner 2009, Cherrill 2010). While adults and mobile juvenile stages of many insect species are capable of behavioural thermoregulation, i.e. raising or lowering their body temperature above / below ambient conditions, the eggs and other immobile stages are likely to be affected directly by climatic conditions, particularly in open habitats whose microclimates are not as buffered as those of taller vegetation (see section 1.5.1 below). Open habitats are also particularly liable to being rapidly and strongly affected by land use changes such as agricultural intensification, eutrophication, or cessation of management (Sutherland and Hill 1995).

The Orthopteran species in Britain display a broad range of biological traits which might explain interspecific differences in responses to environmental change (Benton 2012). A number of species are also wing-dimorphic, i.e. have distinct morphs with radically different wing lengths and corresponding dispersal abilities. This means these species have a large phenotypic plasticity of dispersal, and makes dispersive individuals easily identifiable in the field, rendering them particularly suitable for studies of range expansion processes (Roff 1986, Simmons and Thomas 2004). Orthoptera in Britain are polyphagic or omnivorous, i.e. not bound to single species of food plant and are consequently suitable for investigating effects of environmental changes independent of the presence or absence of specific food plants (Ingrisch and Köhler 1998, Gardiner et al. 2002, Gardiner and Hill 2004, Benton 2012).

1.3.2 Ecological and economic importance

Due to their diversity and abundance, insects are of great ecological and economic importance, performing a large variety of ecosystem roles such as pollination, providing food sources for other species, controlling populations of other animals and plants (where species are carnivorous or omnivorous), seed dispersal, and breaking down and recycling organic matter (Waldbauer 2003). A range of insect species, including several Orthoptera, are also important as a human food source (van Huis et al. 2013). However, some insects can also be significant crop pests, with 15% of crops worldwide estimated to be lost pre-harvest through insects. Climate change is likely to facilitate the spread of some insect pest species to new regions (Yudelman et al. 1998, Maxmen 2013). Globally, some Orthoptera, particularly swarm-forming locusts, can cause considerable damage to agricultural crops during outbreaks, mainly in arid regions. However, close monitoring and early intervention have prevented any devastating large-scale “plagues” for several decades now, and some locusts have in fact suffered regional extinctions (Krall et al. 1998).

None of the Orthopteran species in Europe are currently of significance as pests (Ingrisch and Köhler 1998). As large and abundant insects, temperate Orthoptera can form a large proportion of insect biomass in grassland habitats (Curry 1994) and provide important food sources for threatened, rare or declining bird species such as shrikes (Laniidae), white stork (*Ciconia ciconia*), kestrel (*Falco tinnunculus*), grey partridge (*Perdix perdix*), cirl bunting (*Emberiza cirlus*), corn bunting (*Emberiza calandra*), skylark (*Alauda arvensis*), corncrake (*Crex crex*), and common crane (*Grus grus*), for reptiles such as lizards (Lacertilia), for small mammals such as harvest mice (*Micromys minutus*), and for spiders, especially wolf spiders (Lycosidae) and large web-spinning spiders (Araneidae) (Glutz von Blotzheim et al. 1973-1993, Evans et al. 1997, Ingrisch and Köhler 1998, Brickle et al. 2000, Benton 2012).

Insects, and particularly Orthoptera, are therefore highly suitable, and important, study organisms for investigating effects of climate and land use change. The following sections summarise the scope and main findings of studies on insect range changes to date and highlight some limitations and unresolved questions, which this thesis aims to explore.

1.4 Effects of climate and land use change on insect distributions

This section summarises the main patterns of change which have been observed in insect distributions in recent decades and been attributed to changes in climate and land use. The following section (1.5) then summarises studies of the most important mechanisms and processes involved. Many studies have focussed on a few groups with the best data, particularly butterflies (Thomas 2005). Effects of current climate and land use changes on Orthoptera have been investigated less frequently in large-scale studies, despite the suitability of Orthoptera for such studies, their importance, and even though some long-term monitoring data exist, including in Britain (see section 1.6 below, and chapter 2). Findings across insect groups are summarised in this section and the next in order to provide context for the studies carried out on Orthoptera in this thesis (chapters 3 and 4), suggest potential processes to examine in Orthoptera, and identify open questions which the particular characteristics of Orthoptera may help to investigate further.

1.4.1 Range expansion and aggregation

Poleward range expansions over recent decades have been documented for a number of insect and other species groups, consistent with effects of climatic warming on temperature-limited species distributions (Parmesan et al. 1999, Hickling et al. 2006, Mason et al. 2015). A causal link to climatic warming is emphasised by the fact that average poleward shifts have been greater in studies with greater temperature increases (Chen et al. 2011). Equivalent distributional shifts have also been observed in terms of altitude, with average altitudinal limits of distributions moving uphill in concert with climatic warming over recent decades (Wilson et al. 2007, Chen et al. 2009, Roth et al. 2014).

Averaged across species groups, mean observed distributional shifts may not appear to lag behind expected shifts greatly: for example, across eight insect groups in Britain, average extensions of northern range margins between ca. 1970 and 1995 were 24.3 (SD 10.9) km per decade, compared to expected shifts of 25.7 (SD 4.7) km if species had tracked mean climatic conditions fully (Chen et al. 2011). However, latitudinal as well as altitudinal range changes vary greatly, both within and between species groups, and temperature changes alone do not explain this variation. Some species have exceeded expected range shifts, and others have in fact shifted in the opposite direction, showing that species respond in different ways to the same drivers, and / or that factors other than climate change are involved (Chen et al. 2011, Roth et al. 2014, Mason et al. 2015). The most important such non-climatic factor is likely to be change in land use and the associated changes in spatial distribution and quality of habitats (Burns et al. 2016). Impacts of land use intensification on species distributions have been mostly negative, so they are discussed in the next section.

In addition to expansion of species distributions at their cold range margins, “infill” between spatially separated subpopulations within the latitudinal limits of existing distributions may occur (Wilson et al. 2004). This may be a direct or indirect effect of climatic changes: improved climatic conditions may make previously unsuitable areas habitable (Davies et al.

2006), and / or lead to increasing population densities in existing subpopulations, which in turn lead to density-dependent colonisation of previously unoccupied suboptimal habitats (Oliver et al. 2009).

1.4.2 Range contraction and fragmentation

Range contractions and fragmentations have been observed for many species over recent decades, most commonly attributed to land use changes, but less commonly also to climatic changes, with large interspecific differences in the relative importance of these drivers (Franco et al. 2006, Thomas et al. 2006, Burns et al. 2016). Through conversion and deterioration of habitats in intensively farmed landscapes (section 1.2.3), populations of many species have become restricted to patches of semi-natural habitat and marginal land which is not economical to cultivate. In Britain, distributions of most habitat specialist butterflies shrank significantly between 1970 and 1999, attributed to negative effects of land use changes (Warren et al. 2001). Similarly, the greatest declines among moths in Britain between 1970 and 2010 occurred for species whose caterpillars are associated with low-nitrogen and open habitats, consistent with negative effects of nutrient enrichment, intensification of agriculture and abandonment of marginal land (Fox et al. 2014).

For cold-adapted species, climatic warming may cause extinctions and contraction of the southern / warm range margin. For example, warm range margins of butterflies with a southern limit in Britain have moved northwards and uphill between 1970 and 1999 (Franco et al. 2006), and moth species with a southern range margin in Britain declined significantly between 1970 and 2010 (Fox et al. 2014). Similarly, lower altitudinal range margins of butterflies in Spain have retracted uphill, with higher egg survival at greater altitudes suggesting a causative effect of rising temperatures (Wilson et al. 2005, Wilson et al. 2007, Merrill et al. 2008).

The above summary illustrates that both climatic and land use changes may strongly affect insect distributions. Availability of long-term, large-scale climatic data has allowed many studies to include climate directly as a covariate. Equivalent data for land use change is not often available in sufficient detail or scale, and proxies such as species' resource requirement traits can be used instead to assess likely effects (chapter 3). Many differences in recent distributional changes between species currently remain unexplained. One reason for this may be that most studies have only considered effects of long-term changes in *mean* climate, and not considered annual or seasonal *variability*, even though this is known to strongly affect insect abundances (Pollard and Yates 1993, Roy et al. 2001, Henry et al. 2014) (chapter 4). An understanding of the mechanisms and processes involved in species' responses to environmental change is important to help elucidate differences between species further and understand effects of annual variability – this will be discussed in the next section.

1.5 Mechanisms and processes of insect range changes under climate and land use change

1.5.1 Microclimates, thermoregulation and vegetation structure

1.5.1.1 Microclimates

Microclimates can be defined as climates at the scale at which animals and plants experience them, i.e. generally a scale of millimetres to metres. Microclimates are determined by a range of factors in addition to macroclimate, including topography – particularly aspect and slope of the terrain – as well as soil type, hydrology, and vegetation structure, with macroclimate and vegetation structure in particular subject to annual and seasonal variations (Suggitt et al. 2011). Microclimates are of central importance to insect juvenile development and adult activity, and direct or indirect effects on microclimates are one of the key mechanisms by which changes and variability in climate and land use affect insect populations. An understanding of these mechanisms, and of interspecific differences in microclimatic requirements, is therefore essential for elucidating variations between species in responses to environmental change.

As ectothermic organisms, insects largely rely on environmental warmth for their metabolism and development, although many species can vary their body temperature from ambient conditions through thermoregulation to some extent (see below). Insect metabolic rates generally increase with body temperature, between a species-specific physiological minimum and maximum (Gullan and Cranston 1994). Completion of juvenile development from egg to adult requires a species-specific sum of "biologically useful" warmth within this temperature range, often expressed in units of growing degree days (McMaster and Wilhelm

1997). The speed of juvenile development may accordingly vary significantly with the local microclimate, being quicker in locations and years where the required temperature sums are delivered in a shorter time and species unable to complete development where / when the required sums are not reached. For example, development times from hatching to adult were nearly three times longer for two species of grasshopper widely distributed in Britain (Field Grasshopper *Chorthippus brunneus* and Common Green Grasshopper *Omocestus viridulus*) when reared at 25°C (about 8 weeks) compared to 35°C (about 3 weeks), and neither species was able to complete development at 20°C (Willott and Hassall 1998). Importantly, juvenile survival rates tend to increase significantly with decreasing development times, for example due to reduced losses to predation (Richards and Waloff 1954, Ingrisch and Köhler 1998).

Adult metabolism is similarly affected by temperatures. For example, females may be able to lay eggs in quicker succession, and a greater number overall, at higher temperatures (Willott and Hassall 1998). Apart from increased survival (see above), conditions experienced during juvenile development may also have additional lagged effects on adult fitness, for example nymphs developing under warmer conditions tend to produce heavier adults in several grasshopper species, which in turn are significantly more fecund (Richards and Waloff 1954, Willott and Hassall 1998). Where / when warmer temperatures prevail during both juvenile development and the period of adult reproduction, therefore, the combined effects on fitness can be very large. For example, when four grasshopper species that occur in Britain were kept from hatching to dying under two different temperatures of 30°C and 35°C, overall fitness at the lower temperature was reduced by between 27% (*O. viridulus*) and 88% (Stripe-winged Grasshopper *Stenobothrus lineatus*) (Willott and Hassall 1998). These results also highlight large interspecific differences in sensitivity to temperatures.

In broad terms, therefore, climatic warming is likely to extend the cold range margins of insect species, and to speed up development and increase survival, abundances and fitness within their existing ranges, and effects are likely to vary from year to year depending on variations in weather conditions and their seasonal timing.

In addition to warmth, microclimatic humidity is also important for insects, and for many species the egg and juvenile stages are particularly sensitive to direct desiccation (Ingrisch and Köhler 1998). At the same time, increased humidity may cool microclimates through increased evaporation, so a consideration of both warmth and humidity is likely to be important. Nevertheless, effects of humidity have rarely been considered in studies of climate change impacts on insects (Bale et al. 2002, Morecroft and Speakman 2015) (chapter 4).

1.5.1.2 Thermoregulation

Many insects are able to vary their body temperature from ambient conditions to some extent through physiological and / or behavioural thermoregulation. The former includes raising body temperatures through contraction of flight muscles (vibrating the wings) prior to take-off (Gullan and Cranston 1994). Orthoptera do not seem to be able to generate much heat physiologically, and behavioural thermoregulation is their main means of varying temperatures from environmental conditions (Benton 2012). Thermoregulatory behaviours include basking by moving into direct sunlight, orienting the body perpendicular to the sun and positioning legs and wings so as to maximise exposure of the body. To avoid overheating, insects may raise their body off the ground on stretched legs, or seek shade and cooler microclimates by retreating to taller vegetation, if available in sufficient proximity. Some butterflies and locusts also prevent overheating during flight by alternating between active flight and gliding (Gullan and Cranston 1994, Benton 2012).

There are large interspecific differences in thermoregulatory ability. A field study comparing four species of grasshopper in Britain, *C. brunneus*, *O. viridulus*, *S. lineatus* and Mottled Grasshopper *Myrmeleotettix maculatus*, found that at low ambient temperatures the former two were able to raise their body temperatures more than the latter two. For example, at ambient microclimatic temperatures of 15 to 19.9°C, *C. brunneus* achieved a mean elevation of body temperature over ambient of over 7°C, but *M. maculatus* of less than 3°C. On the other hand, at high ambient microclimatic temperatures of 35 to 39.9°C, *O. viridulus* was less able to reduce heat uptake than the other three species, with mean elevations of 4.2°C, compared to less than 1°C for the others. Given that temperatures only slightly above the physiological optimum of 35 to 40°C for all these species can be lethal, *O. viridulus* may therefore be at risk of overheating where microclimates can reach such temperatures. Overall, therefore, thermoregulatory ability enables *C. brunneus* and *O. viridulus* to occupy cooler microclimates than the other two species, but restricts *O. viridulus* at the warm end of the spectrum (Willott 1997).

The immobile life stages of insects, particularly eggs, are not able to thermoregulate behaviourally and are therefore more directly dependent on ambient microclimatic conditions. Adult insects may vary oviposition sites to some extent depending on prevailing microclimates at the time of oviposition (Merrill et al. 2008), but eggs are then dependent on ambient conditions until they hatch. Oviposition sites and microclimatic requirements of eggs are therefore likely to be important determinants of habitat suitability for many species (Ingrisch and Köhler 1998). In addition, the variability and sequence of seasonal weather patterns from one year to the next is likely to potentially affect species.

1.5.1.3 Vegetation structure

Short vegetation produces significantly greater microclimatic extremes – heating up more quickly and reaching greater maxima, but also cooling down more quickly and reaching lower minima – than taller vegetation, which buffers microclimates (Suggitt et al. 2011). In addition, taller vegetation tends to create more humid microclimates through increased evaporation and reduced airflow.

Shorter vegetation therefore typically creates microclimates that deliver greater annual sums of biologically useful warmth (section 1.5.1.1). Species' microclimatic requirements and thermoregulatory ability may consequently restrict them to particular vegetation structures (Willott 1997, Thomas et al. 2009). Where species are warmth-limited (for example near their cold range margins), macroclimatic warming may therefore create warmer microclimates in taller vegetation than was previously occupied, with effects modulated by annual variability in weather conditions. There is evidence for several species that, concurrent with recent climatic warming, they have begun to utilise habitats with microclimates that were previously too cool, e.g. taller vegetation (Pateman et al. 2012), or cooler topographic aspects (Davies et al. 2006). Similarly, greater proportions of butterfly individuals were found in cooler, closed habitats in hotter years and regions, compared to cooler years and regions (Suggitt et al. 2012).

Vegetation structure, in turn, may be strongly influenced by land use as well as macroclimate, particularly the balance of precipitation and warmth, and their seasonal timing (Carey et al. 2008, Parton et al. 2012). Increases in vegetation height through climatic or land use changes may lead to locally cooler microclimates, despite concurrent macroclimatic warming (Wallisdevries and Van Swaay 2006). Similarly, macroclimatic regional or seasonal drought, or changes in hydrology or soil moisture may lead to regionally and / or seasonally hotter and more extreme microclimates by stunting vegetation growth.

1.5.1.4 Conclusions

Information about interspecific differences in microclimatic requirements helps to understand variations between species in their responses to environmental change. However, while microclimatic requirements and thermoregulatory ability of many insect species are becoming better understood, standardised measurements are still rarely available across entire species groups. Therefore, inclusion of proxies for species' microclimatic requirements in analyses, such as position of the northern range margin, preferred vegetation structure, and habitat specificity may help to explain differences between species. Microclimates themselves are determined by a complex interplay of factors including macroclimate (temperature, precipitation), land use, hydrology, and vegetation structure, and detailed measurements of microclimates are not usually available at large scales. They are therefore still challenging to include in large-scale analyses of effects of environmental change. Where possible, measurements of the main factors influencing microclimates, or proxies for them, are likely to be important to include in analyses, for example macroclimatic temperature *and* precipitation, or measures of changes in vegetation height, management intensity, or nutrient deposition. Yet, as indicated in the previous section, few studies have considered effects of precipitation. Similarly, annual variability and seasonal timing of weather conditions is likely to be important, but most studies have only considered trends in long-term means.

Variations in local and seasonal microclimates through changes in macroclimate and land use may lead species to move from current habitats to new ones – in order to escape deteriorating conditions and / or utilise developing opportunities. Species' ability to disperse through the landscape will influence their overall distributional responses to environmental changes. Influences of climate and land use change on the dispersal process will be discussed in the next sections.

1.5.2 Dispersal

Dispersal is a fundamental process influencing species' ability to respond to environmental changes by changing their distributions. Investigations of interspecific differences in dispersal ability and dispersal processes, and how they are affected by changes in climate and land use may therefore elucidate variations in responses to these drivers.

The dispersal process can be subdivided into three phases: emigration, transition and settlement (Clobert et al. 2012); the first two are discussed here, and settlement in the next section (1.5.3). Emigration is likely to be dependent on population density in many cases, affecting both the potential propagule size (number of individuals available to emigrate) and the individual-level propensity to disperse (Travis and Dytham 2012). For example, a majority of studies of wing-dimorphic Orthoptera have found a positive association between population densities and development of long-winged, dispersive individuals (macropters) (Ingrisch and Köhler 1998, Behrens and Fartmann 2004, Poniatowski and Fartmann 2011c). Similarly, a study of butterfly abundances and distributions showed that stable or increasing abundances are a precondition for range expansions (Mair et al. 2014), and another study found higher rates of emigration from plots with experimentally raised butterfly densities than from lower-density plots (Enfjäll and Leimar 2005). On the other hand, negatively density-dependent dispersal has also been observed in some studies (Kuussaari et al. 1996, Simmons and Thomas 2004). Evolutionary reasons for both scenarios have been proposed, such as avoidance of intraspecific competition and of inbreeding leading to emigration from high-density populations; and conspecific attraction, in order to increase the chances of mating, leading to emigration particularly from very low-density populations and immigration to higher-density populations. Conspecific attraction could also stem from higher densities reflecting higher underlying habitat quality (Hanski 1999, Enfjäll and Leimar 2005). Effects of environmental changes on population densities are therefore important to consider in studies of range changes where such data is available or can be collected. No abundance data are currently available for Orthoptera in Britain at large scales, and collection of such data in future would greatly enhance opportunities for such research (chapter 5).

There is no doubt that many insects are very effective dispersers, as the annual observations of migrant insect species which have crossed seas or mountain chains indicate. However, direct investigations of the transition (movement) phase of insect dispersal are still technologically challenging due to the difficulty of tracking individuals over large distances and it is therefore hard to investigate differences between species directly. Tethered flight experiments have measured potential dispersal ability of moths and documented significant interspecific differences (Jones et al. 2016). Other studies have used proxies for dispersal, such as the frequency with which insects cross habitat boundaries, to assess dispersive potential, and have also observed significant differences between species (Haddad and Kingsolver 1999, Kallioniemi et al. 2014). For Orthoptera, mark-release-recapture studies have observed dispersal distances up to several hundred meters, and significant differences between species (Ingrisch and Köhler 1998). However, this method is suited to detecting dispersal events up to a few hundred meters at most. Other methods have inferred much larger potential dispersal distances, for example investigation of the genetic similarity of macropterous males of *M. roeselii* to surrounding source populations suggested mean dispersal distances of 8.0 ± 1.3 km (Hochkirch and Damerau 2009). Similarly, flight tunnel experiments showed that macropters of *C. discolor* flew 12.3 ± 2.1 km to exhaustion in a single sitting (Simmons and Thomas 2004). Comparable measurements do not exist for most species, and for comparative analyses of whole species groups, proxies for dispersal ability such as wing load have to be used (Hill et al. 1999). For example, a study of distributional changes in British butterflies between 1970 and 1999 found that a mobility index (and habitat specificity, with which it was highly correlated) was an important predictor of whether species' distributions had expanded or contracted (Warren et al. 2001).

Apart from species' dispersal ability, environmental factors may also influence actual dispersal distances. As with dispersal distances, direct investigations of how environmental factors affect dispersal of different insect species are challenging due to the difficulty of tracking dispersing insects, and have not often been attempted. A detailed study of immigration of Diamond-backed moths *Plutella xylostella* into Britain in 2000, using vertical-looking radar, high altitude aerial netting, and light traps, suggested that the moths flew from continental Europe during a period of particularly warm nights with following easterly winds, and at heights above ground corresponding to warm layers of air on the nights in question (Chapman et al. 2002). Such direct investigations require a large technological effort, which few other studies have attempted, or they have only considered short movement distances. For example, daily movement distances of grasshoppers through a field were found to depend strongly on maximum daily temperatures during the adult period (Walters et al. 2006). More generally, insect flight activity is known to be strongly influenced by ambient temperatures (Pollard 1977, Uvarov 1977). However, as stated in the previous sections, most studies investigating the role of environmental factors in distributional changes have only considered changes in mean climatic conditions, not their annual or seasonal variability (Henry et al. 2014). Wing-dimorphic insects are a useful study system in this context, because environmental effects on development of macropters can be investigated. These can then be taken as a proxy for impacts on dispersal distances, because macropters are known to be capable of significantly greater dispersal distances than brachypters. For example, in the above-mentioned flight tunnel experiment, the distance that macropters flew (12.3 ± 2.1 km) was three orders of magnitude greater than the distance for brachypters (0.02 ± 0.01 km) (Simmons and Thomas 2004).

This section has highlighted the importance of understanding factors which influence the dispersal process of species in order to understand interspecific differences in responses to environmental change: environmental effects on population abundances, which may increase emigration; species' dispersal abilities; and environmental factors affecting the transition phase. In turn, the dispersal distances required for successful expansion of a species depend on the spatial arrangement of suitable habitat, and suitability of habitats for the third phase of dispersal – colonisation – depends on the requirements of each species, and may vary with environmental conditions, such as climate. These factors are the subject of the next section.

1.5.3 Habitat fragmentation, colonisations and extinctions

Recent history has seen the loss and fragmentation of many habitats, and populations of associated species, due to land use changes and, particularly at warm range margins, climatic changes (sections 1.2.3 and 1.4.2). The ability of species to expand or shift their distributions in fragmented landscapes depends on the balance between their dispersal ability and the distances between suitable habitat patches: only if species are sufficiently mobile, or generalist in their habitat requirements, or both, are they able to spread successfully through the landscape. At the same time, poor dispersers and habitat specialists may not be able to expand their distributions, if distances between suitable habitat patches are too large for successful colonisation – even if climatic warming is making patches suitable for occupation beyond the current distributions. Such a combination of the effects of simultaneous land use and climate change is consistent with the observation that in Britain, distributions of most habitat specialist butterflies have shrunk significantly between 1970 and 1999, while half of the mobile habitat generalists have expanded their ranges (Warren et al. 2001, Fox et al. 2015). Even where species are able to expand, habitat availability may limit the rate of spread: a study of the Speckled Wood butterfly *Pararge aegeria*, found that expansion rates were significantly greater in a region with more suitable habitat than in another region with less habitat, even though the latter was further south (Hill et al. 2001).

The majority of Orthoptera species in Britain have a northern range margin here, with the distributions of only a handful of species reaching the northern edges of Scotland (Haes and Harding 1997). Climatic warming over recent decades would therefore be expected to allow the majority of species to expand their distributions northwards, yet, while several species have done so, there are large variations between species and many have not (Mason et al. 2015). No studies have so far assessed the factors influencing these interspecific differences at a national scale (chapter 3).

Populations consisting of multiple subpopulations in distinct habitat patches have been termed “metapopulations” (Levins 1969, 1970, Hanski 1999). While Levins’ idealised metapopulations (with all subpopulations equally liable to periodic extinction and depending on each other for long-term persistence) seem to be rare in reality, “mainland-island metapopulations” with larger core populations and smaller satellites are commoner, and many species with localised habitats show aspects of metapopulation dynamics during distributional changes (Harrison 1991). Metapopulation models have proved useful in investigating processes of colonisation, extinction and dispersal between subpopulations in such fragmented distributions, and suggest that both the total amount of habitat, and the degree of fragmentation, are likely to influence persistence of species in the landscape, particularly where total amounts of habitat are small. Effects of fragmentation vary between species: for species of formerly “land-covering” habitats such as woodlands, effects begin to become apparent when habitat cover falls below approximately 20-30% of the landscape, but for species of naturally sparse habitats, which are adapted to fragmentation, effects may appear only at considerably smaller percentages (Rybicki and Hanski 2013, Hanski 2015).

Climatic warming may make microclimates in additional habitats suitable, reducing dispersal distances between patches of suitable habitat and making the landscape more permeable for the species concerned (Davies et al. 2006, Oliver et al. 2009, Pateman et al. 2012). Land use change may have a similar effect, for example one study suggests increased availability of tall grassland on farmland, due to subsidies encouraging land to be taken out of cultivation, was important to the range expansion of a bush-cricket in Britain (Gardiner

2009). Studies of colonisation process suggest that “propagule pressure”, i.e. the number of colonists arriving, is an important factor for successful settlement (Williamson 1996). Numbers of colonists are likely to depend strongly on the degree of habitat fragmentation in the landscape, with small, isolated patches of habitat less likely to receive sufficient propagules for successful colonisation.

For other species, particularly habitat specialists, land use change may make fewer habitat patches suitable, leading to greater fragmentation and increased distances between habitat patches, rendering the landscape less permeable for dispersing individuals (Fox et al. 2014). As distributions decline and fragment, individual populations become smaller, making them increasingly susceptible to extinction through stochastic environmental disruptions (MacArthur and Wilson 1967, Hanski 1999). Stochastic environmental effects have less often been considered in the context of colonisations. However, it is likely that annual and seasonal variations in environmental conditions affect not only emigration and dispersal, but also successful establishment at new sites (chapter 4).

This section has illustrated that the balance between a species’ dispersal ability, its habitat requirements, and the spatial distribution of suitable habitats in the landscape determine the ability of individuals to move between habitat patches. This includes the colonisation of new sites, leading to expansions of distributions, and studies of these factors may therefore help to understand interspecific differences in responses to environmental change. However, species’ dispersal traits may vary significantly within, as well as between, species (Stevens et al. 2010). This may be due to evolutionary processes during range changes, and an understanding of these may therefore also help to explain variations in species’ responses. Evolutionary processes during range changes are not directly investigated in this thesis, but a brief account is given in the next section for context and to aid interpretation of findings.

1.5.4 Evolutionary processes during range changes

Theoretical models and empirical observations both suggest that evolutionary processes occur during sustained range changes (Hill et al. 2011, Travis and Dytham 2012). The dispersal process leads to selective breeding of dispersive individuals at newly colonised sites. If range expansions are sustained over several generations, this leads to evolution of increased dispersal in a positive feedback loop. For example, a study of two rapidly expanding wing-dimorphic bush-crickets in Britain observed greater numbers of dispersive macropters at range margin field sites compared to the range core. When reared in the lab under common environmental conditions, significantly greater proportions of range margin individuals developed into macropters, suggesting a higher propensity for dispersal had evolved during the range expansion process. In addition, when tested in a wind tunnel, macropters of the Long-winged Conehead *Conocephalus discolor* reared from range margin populations flew significantly further (16.7 ± 2.3 km) than macropters from range core populations (4.2 ± 0.8 km) (Thomas et al. 2001, Simmons and Thomas 2004). Altogether, therefore, both emigration rates and dispersal distances had increased through evolution during the range expansion process. The study also found strong trade-offs between dispersal and reproduction, with macropters producing significantly fewer eggs and smaller spermatophores than brachypters, providing a likely evolutionary explanation for the observation that the changes towards increased dispersal are reversed within 5-10 years of colonisation of a site. Evidence for comparable evolutionary changes of flight morphology or dispersiveness has also been found for butterflies (Hill et al. 1999, Hanski et al. 2002) and damselflies (Hassall et al. 2009). Dispersal ability may therefore change within species over time and space.

Among butterflies, positive correlations between dispersal ability and habitat generalism have been observed, with generalists being mobile, and the majority of habitat specialists having low dispersal abilities (Haddad and Kingsolver 1999, Warren et al. 2001). It is likely that this correlation is at least partly adaptive in a fragmented landscape, because for habitat specialists to leave patches of suitable habitat is more risky, as the chances of finding another suitable patch may be low, while for generalists the risks are lower and opportunities may be greater (Mair et al. 2015). For habitat specialists, this may be a vicious circle in fragmented landscapes, with spatial isolation of habitat patches selecting against dispersal, leading to increasing genetic isolation (Saccheri et al. 1998). On the other hand, there is evidence that in some cases climatic warming can facilitate evolution of wider habitat tolerances and changes in host plant preference (Pateman et al. 2012).

1.6 Citizen science for distribution data

The above review indicates the importance of long-term, large-scale monitoring data of insect distributions and abundances in understanding effects of climate and land use change on species. A successful, and arguably the only practical, way to collect such data is with the help of volunteers – an approach now often referred to as “citizen science”. This section briefly reviews the suitability of citizen science for biological recording, its strengths and weaknesses in providing data for scientific use, and the current availability of large scale datasets in Britain.

1.6.1 Participation and motivations

Biological recording by naturalists has a long history, and has informed scientific research for many generations. Now often referred to as “citizen science”, such recording by volunteers has proved very effective: many of the most important long-term datasets have been created in this way, and specimens collected by naturalists have contributed significantly to many museum collections (Miller-Rushing et al. 2012). In Britain, biological recording has a particularly strong tradition, and has grown from the time of John Ray, whose catalogue of the plants of Cambridgeshire was published in 1660 (Oswald and Preston 2011), to the present day, with over 200 million records publically available on the National Biodiversity Network Atlas (National Biodiversity Network 2017).

There seem to be several reasons why voluntary biological recording attracts such a dedicated following and can be so effective for large-scale monitoring projects. Most importantly perhaps, it is simply an enjoyable way for many people to engage with the natural world and with the species they love (Tweddle et al. 2012). For many species groups and projects, contributors from a basic level of expertise upwards can make useful contributions, and recording is a means for participants to find out and learn more about the species in question, and for people concerned about changes in the natural world to get involved in its study and conservation, while gaining insights into research processes (Bonney et al. 2009, Miller-Rushing et al. 2012). From the point of view of funders and those who need and use the collected data, such as research organisations, government conservation bodies, planning departments, and conservation charities, citizen science can be a cost-effective way to achieve a wide coverage of data collection over large areas and long time periods, which would be unaffordable without the involvement of volunteers. The value of the time spent by volunteers in Britain on structured biological surveys alone is conservatively estimated at £8.6 million per year – many times more than the funding invested in running the surveys (National Biodiversity Network 2015). Globally, annual in-kind contributions by volunteers to biodiversity citizen science projects are conservatively estimated at between $667 million and $2.5 billion (Theobald et al. 2015).

Despite concerns that interest in the natural world is declining through processes like increasing urbanisation, volunteer support for biological recording remains strong. In fact, increasing leisure, mobility and incomes over the second half of the 20th century as well as increasing human population numbers generally are likely to have contributed to observed increases in participation in many citizen science projects (Miller-Rushing et al. 2012, Preston et al. 2012). Technological developments in communications and computing have made the collection, sharing and analysis of records easier and have created new opportunities, such as the use of sensors during record collection, quick feedback, and automated support for record validation (Silvertown 2009, August et al. 2015a).

1.6.2 Biases and analysis of citizen science data

Scientific use of biological recording data has a long tradition, ranging from Charles Darwin's examination of patterns of Vice County distribution records of plants in the "Origin of Species" (Darwin 1859) to recent investigations of climate change impacts on the natural world (IPCC 2014), and assessments of species threat statuses (Mace et al. 2008, IUCN 2012). Citizen science projects vary widely in the scientific rigour of data collection, from unstructured collection of single observations by the public to structured monitoring of species with a standard protocol and repeat visits by trained naturalists (Preston et al. 2012, Pocock et al. 2017). In addition, in long-term projects methods of data collection, sharing and storage may change considerably over time (Preston et al. 2012). The unstructured nature of recording in many projects, changes in recorder behaviour over time, and changes in technologies for recording and data processing, mean that data collected by many citizen science projects are subject to multiple biases, such as variation in recording effort over time and space (Isaac et al. 2014, Isaac and Pocock 2015). These biases have to be taken into account during data analysis, and a range of statistical methods have been developed for this purpose, which make different assumptions about recorder behaviour and account for them accordingly (Isaac et al. 2014). A thorough understanding of a project's history and the evolution of its data collection protocols is important for identifying biases, selecting appropriate methods for data analysis, and setting up analyses in ways which ensure that the assumptions made are likely to be met (this is explored in more detail in chapter 2 of this thesis).

Citizen science projects need to strike a balance between the interests of volunteers and users of the data, and there is often an associated trade-off between the quantity and quality of the data collected. For example, opportunistic recording of distributions has the advantage of being non-prescriptive, allowing recorders to record what and where they like, and expending as much or as little time as they choose. As such it is very popular, and therefore often achieves greater participation than highly structured and prescriptive survey methodologies (Preston et al. 2012, Tweddle et al. 2012). Where sampling protocols are prescriptive and rigorous, the data collected is likely to be of higher quality, but projects may achieve smaller sample sizes and more limited spatial and temporal coverage, reducing the likelihood of the data being put to scientific use (Stanbury et al. 2015, Theobald et al. 2015). Increases in computing power and developments in statistics increasingly allow analysis of larger and less standardised datasets, and it is also becoming possible to combine analysis of structured and unstructured datasets (Pagel et al. 2014, August et al. 2015a). Nevertheless, the degree of standardisation of record collection remains an important consideration in citizen science projects.

1.6.3 Data availability

While species-richness makes insects suitable for comparative studies of impacts of environmental change (section 1.3.1), it also poses problems for monitoring, and few insect groups have detailed monitoring data for whole regions and long time periods (Thomas 2005). Britain is one of the best-surveyed regions globally, and unstructured distribution data have been collected here for a range of insect groups for several decades, at least at coarse spatial and temporal scales (Roy et al. 2014). Very few insect groups have systematic, detailed abundance monitoring data at large spatial and temporal scales. Among the exceptions are butterflies and moths in Britain (Rothamsted Insect Survey 2017, UK Butterfly Monitoring Scheme 2017), and those groups for which such data are available have proved extremely fruitful for research into species' responses to environmental changes.

Distributions of grasshoppers and crickets have been monitored in Britain by a dedicated recording scheme since 1968 (Marshall and Haes 1988). Recording is unstructured, and has aimed at national coverage at a 10km square resolution for the purposes of national atlases, and at finer resolutions for county atlases (chapter 2). There is no standardised abundance monitoring data for Orthoptera at large scales, and currently no standard protocol for collecting such data (chapter 5).

1.6.4 Conclusion

The involvement of volunteers in the collection of biological records has proved effective for monitoring species distributions over large areas and long time periods. In order to be inclusive and achieve wide participation, many citizen science projects have loose data collection protocols with limited standardisation, leading to biases in the datasets, which need to be taken into account during analysis. Statistical methods for analysis of such data have been improving. However, appropriate methods need to be selected for each dataset, and a thorough understanding of a project's data collection processes is important in order to ensure that the assumptions made by each method are heeded.

Britain has a strong tradition of biological recording, and distributions of many insect groups have been recorded over several decades. However, scientific analysis has tended to focus on only a few groups with the best data, particularly butterflies and moths. A long-term recording scheme has monitored distributions of Orthoptera in Britain since 1968, but few studies have analysed the data in detail to date and these have been limited to a few species or regions (Simmons 2003, Gardiner 2009, Cherrill 2010). This is beginning to change (Eaton et al. 2015, Oliver et al. 2015a, Hayhow et al. 2016). Nevertheless, there is an opportunity to analyse existing Orthoptera data more, and to consider development of abundance monitoring for this popular group.

1.7 Thesis: aims, main questions and layout

Climatic and land use change are affecting the distributions of species in many regions and habitats, and are set to continue doing so throughout this century and beyond. A detailed understanding of species' responses is critical for conservation and adaptation planning, but many interspecific differences in range changes remain unexplained. Studies of climatic impacts have tended to investigate mean changes in climate, disregarding annual variability. As ectothermic insects of open habitats, Orthoptera are a sensitive study system for the effects of climatic and land use changes. They can constitute a large proportion of insect biomass, giving them particular significance for conservation. The Orthopteran species in Britain have a variety of biological and ecological traits, and include several wing-dimorphic species, making dispersive individuals easily identified in the field; they are therefore a particularly suitable taxonomic group for investigating distributional changes. *The first main aim of this thesis is to investigate interspecific differences in recent range changes of Orthoptera in Britain, and the effects of climatic change and climatic variability on the pattern and process of dispersal and colonisation of two rapidly expanding species*.

Britain has a remarkable tradition of biological recording by volunteers, allowing changes in distributions of multiple taxonomic groups to be studied over large areas and long periods of time. Methods of recording, archiving and analysing the data have changed considerably over time, including through technological developments. *The second main goal of this thesis is to review and evaluate the available Orthoptera recording data in Britain, and the scope for development and expansion of Orthoptera monitoring in future in order to maximise its usefulness for conservation and research*.

Based on these two aims, the PhD project addresses the following specific questions:

1) Inter- and intraspecific variability in responses to climate and land use change:

- What distribution changes have occurred over recent decades for Orthopteran species, and which life history, resource use, dispersal and distributional traits are important in explaining them? What implications do the inferred relationships have for future predicted range changes in this and other taxonomic groups?

- What are the annual colonisation rates of the two most rapidly expanding species, and how are they affected by seasonal weather conditions? Does seasonal weather affect the rates of long-wingedness in these species (the main mechanism for dispersal)?

2) Evaluation and scope for development of Orthoptera recording for research purposes:

- How have Orthoptera distributions been monitored in Britain over recent decades? What are the characteristics and biases of the data produced and how can they be analysed to assess trends in distributions?
- What would be a suitable method for structured abundance and site monitoring of Orthoptera by volunteers? How many participants would such a monitoring scheme need in order to detect given levels of abundance change?

The thesis is structured as follows: Chapter 2 critically reviews the Orthoptera Recording Scheme and its data, and methods for analysis of trends in distribution. Chapter 3 employs one of these methods to calculate distribution trends for all Orthopteran species in Britain, and links them to biological traits to understand whether traits affect species' responses to climate and land use change. Following on from this, Chapter 4 assesses the influence of seasonal weather on the process of dispersal and colonisation of the two most rapidly expanding species. These two species display wing-length dimorphism, and field counts of dispersive individuals at sites near the expanding range margins over five years were also used in this analysis. In light of limitations of current Orthoptera recording data for answering the kinds of ecological questions set out in Chapters 3 and 4, Chapter 5 assesses the feasibility of structured Orthoptera abundance and site monitoring by volunteers, with a view to improving data quality for, and the potential scope of, a broad range of future research. The final Chapter 6 discusses the findings of this thesis together and explores ideas for further research.

2. Critical overview of Orthoptera Recording Scheme data

2.1 Abstract

The Orthoptera and Related Species Recording Scheme has been monitoring distributions of grasshoppers, crickets and related insects in Britain and Ireland since 1968 and has built up a large database of records. This PhD project analyses these data to investigate interspecific differences in species' responses to environmental changes over recent decades. This chapter provides an overview of the Scheme's evolution and critically reviews its data collection and collation processes, including associated biases in the data. Three statistical methods developed to extract distribution trends from data of this type, while taking into account the multiple associated biases, are applied to the scheme's data and compared.

Recording is mostly carried out by volunteers, and is generally unstructured and "presence only", with no explicit measure of recording effort and no recording of "absences", although five national, and over thirty county, atlases have attempted to compile comprehensive distributional information at different spatial scales, and at temporal scales of several years or decades. Traditional recording on paper cards has gradually given way to digital, online, and – increasingly – mobile, systems, with concurrent increases in the spatial and temporal precision of records. Accessible, high quality identification resources have become increasingly available, and digital systems facilitate quality control of records by scheme coordinators and feedback to recorders. Numbers of records received by the scheme have increased significantly over time, with large regional variations.

Example distribution trends were calculated with three statistical methods developed for unstructured data of this type, a "relative range change index", and "reporting rate" and "occupancy detection" models. The assumptions made by each method are spelled out and consideration is given to how analyses can be set up in order to meet them. When the three methods are applied to the data and interpreted with care, results of all three are similar. The relative range change index is suitable for the largest range of data quality and quantity and therefore applicable to the largest number of species, but has limited statistical power;

occupancy detection models are the most robust and powerful measure but require a higher quality and quantity of records than the range change index.[1]

2.2 Scope and operation of the recording scheme

This section reviews the evolution of the Orthoptera recording scheme's scope and operation, in order to understand the structure and biases of its data and appropriate methods for data analysis, which are explored in the subsequent sections.

2.2.1 Establishment, coordination and volunteer basis

The Orthoptera Recording Scheme was launched in 1968 at the Biological Records Centre (BRC) with the aim of mapping and monitoring the distributions of Orthoptera and related orders in Britain and Ireland at a 10x10km grid square resolution. The majority of records are field observations from volunteer recorders, and additional records are collated from other sources such as publications and museum collections. For the first ten years the scheme was run directly from BRC, before being devolved as a separate entity in 1977, like other national recording schemes, but BRC has continued to support the scheme and host its data holdings throughout. The scheme has been coordinated nationally by John Heath and Michael Skelton (1968-77, at BRC), Chris Haes (1977-95), John Widgery (1996-2002), Peter Sutton (2003-

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[1] *The author has been joint coordinator of the Orthoptera recording scheme since 2008 and has contributed to the following aspects of the scheme discussed in this chapter: iRecord Grasshoppers app (conception of idea, applications for funding, sourcing and preparation of most contents, oversight of project); data collation (63,135 records in 62 datasets); online verification of records (9,568 records); communication with recorders (minimum approx. 2,000 emails; creation of scheme email contacts list); recruitment of county recorders; newsletters (all contents 2013 issues, majority of contents 2014-16 issues); identification literature (downloadable guides to common species); identification courses or talks (6 events); scheme social media (setting up and running scheme Twitter account; Facebook posts on entomological groups); scheme website (contribution to creation of initial contents in 2008; majority of contents and contribution to maintenance 2009-17); annual Royal Entomological Society Orthoptera Special Interest Group meetings (convenor since 2013).*

present) and Björn Beckmann (2008-present, at BRC). National coordinators have been supported by "county recorders" coordinating recording for Orthoptera in many counties, often in association with Local Environmental Record Centres.

2.2.2 The British and Irish species

There are currently 30 Orthopteran species established in the wild in Britain: 11 bush-crickets (Tettigoniidae), 5 crickets (Grylloidea), 3 groundhoppers (Tetrigidae) and 11 grasshoppers (Acrididae). 13 of these are established in Ireland, and 19 plus a further two species of grasshopper in the Channel Islands (Table 2.1). In addition, the recording scheme covers related insect orders: in Britain there are currently 3 species of earwig (Dermaptera) established in the wild, 4 cockroaches (Dictyoptera), and 3 stick-insects (Phasmida) (not included in Table 2.1). Apart from species established in the wild, there are occasional records of several introduced or migratory species which only survive for a limited time, or only indoors, and do not currently have established populations in the wild (not included in Table 2.1).

Table 2.1: Orthopteran species established in the wild in Britain, Ireland and the Channel Isles

Species group	Family	Species	Common Name	established in		
				Britain	Ireland	Channel Isles
Bush-crickets	Tettigoniidae	*Meconema thalassinum*	Oak Bush-Cricket	x	x	x
		Meconema meridionale	Southern Oak Bush-Cricket	x[1]	x[1]	
		Tettigonia viridissima	Great Green Bush-Cricket	x		x
		Decticus verrucivorus	Wartbiter	x		
		Pholidoptera griseoaptera	Dark Bush-Cricket	x	x	x
		Platycleis albopunctata	Grey Bush-Cricket	x		x
		Metrioptera brachyptera	Bog Bush-Cricket	x		
		Metrioptera roeselii	Roesel's Bush-Cricket	x	x	x
		Conocephalus discolor	Long-winged Conehead	x		x
		Conocephalus dorsalis	Short-winged Conehead	x	x	x
		Phaneroptera falcata	Sickle-bearing Bush-Cricket	x[2]		
		Leptophyes punctatissima	Speckled Bush-Cricket	x	x	x
Crickets	Gryllidae	*Gryllus campestris*	Field Cricket	x		x
		Nemobius sylvestris	Wood Cricket	x		x
		Oecanthus pellucens	Tree Cricket	x[3]		x[3]
	Mogoplistidae	*Pseudomogoplistes vicentae*	Scaly Cricket	x		x
	Gryllotalpidae	*Gryllotalpa gryllotalpa*	Mole Cricket	x		x
Ground-hoppers	Tetrigidae	*Tetrix ceperoi*	Cepero's Groundhopper	x		x
		Tetrix subulata	Slender Groundhopper	x	x	x
		Tetrix undulata	Common Groundhopper	x	x	x
Grass-hoppers	Acrididae	*Oedipoda caerulescens*	Blue-winged Grasshopper			x
		Stethophyma grossum	Large Marsh Grasshopper	x	x	
		Stenobothrus lineatus	Stripe-winged Grasshopper	x		
		Stenobothrus stigmaticus	Lesser Mottled Grasshopper	x[4]		
		Omocestus rufipes	Woodland Grasshopper	x		
		Omocestus viridulus	Common Green Grasshopper	x	x	
		Chorthippus brunneus	Field Grasshopper	x	x	x
		Chorthippus vagans	Heath Grasshopper	x		x
		Chorthippus parallelus	Meadow Grasshopper	x		x
		Chorthippus albomarginatus	Lesser Marsh Grasshopper	x	x	
		Euchorthippus elegantulus	Jersey Grasshopper			x
		Gomphocerippus rufus	Rufous Grasshopper	x		
		Myrmeleotettix maculatus	Mottled Grasshopper	x	x	

[1] temperate European species, established in Britain since ca. 2001, in Ireland since ca. 2008

[2] temperate Eurasian species, established in Britain since ca. 2015

[3] southern-temperate Eurosiberian species, established in Britain since ca. 2014, in the Channel Isles since ca. 2010

[4] Isle of Man only

The highest Orthopteran species richness occurs in the south and east of Britain, with over 10 species recorded per hectad in many areas, reaching 25 species in the most diverse square. There is a strong negative gradient in species richness towards the north (and west) of Britain, with most species reaching their northern distributional limit somewhere within

Britain, and only four species occurring in the northern parts of Scotland (Fig. 2.1). This pattern is likely to be reinforced to some extent by recording effort, with the highest human population and recorder densities in the south-east (see section 2.2.2 below). Recording effort in Ireland is very sparse in many areas.

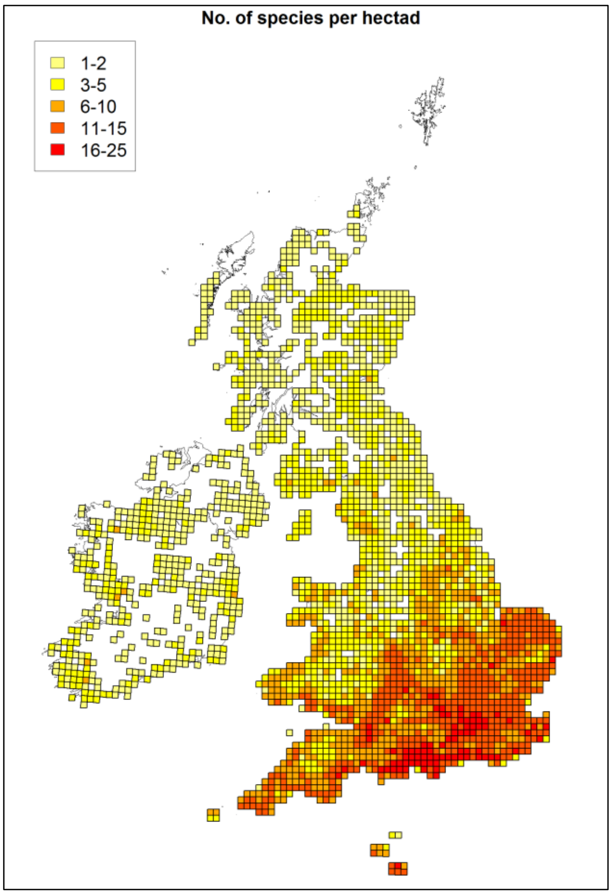


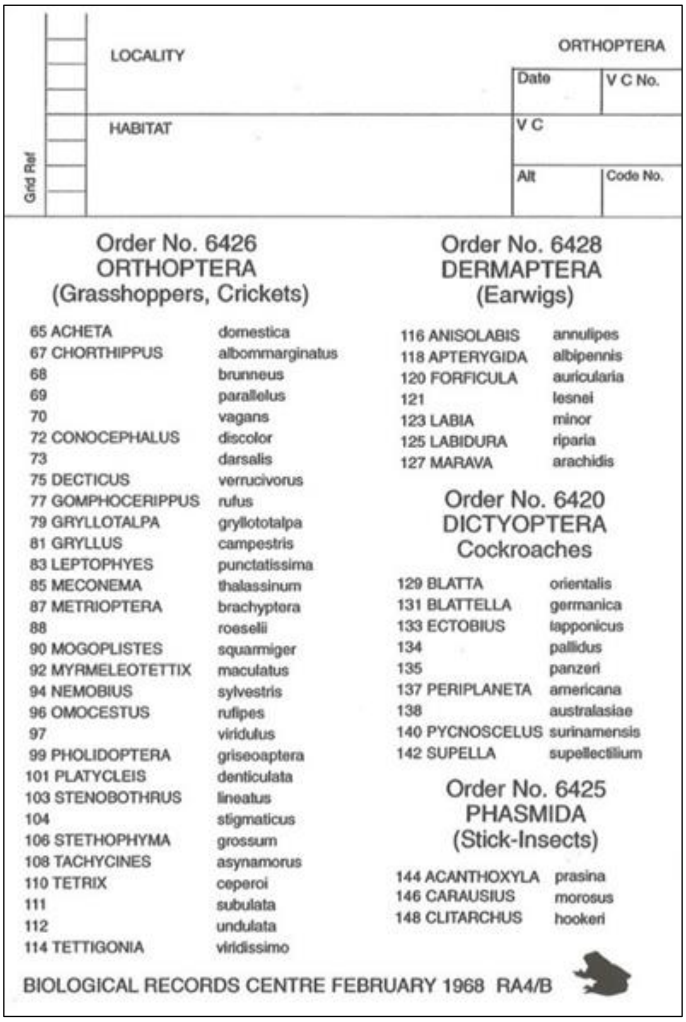
Fig. 2.1: Orthoptera species richness in Britain, Ireland and the Channel Islands. Squares are coloured by the number of species recorded per 10x10km square (hectad) in the Orthoptera recording scheme database across all years.

2.2.3 Evolution of recording methods

2.2.3.1 Recording cards

For the first decades of the recording scheme's operation most recording was carried out on bespoke paper recording cards. These were designed to be used both in the field and subsequently stored as an archive. Standard fields allowed entry of location information (grid reference, locality name, Watsonian Vice County number, habitat information and altitude), visit information (date, recorder name / code), and species presence, which was recorded by crossing names off a complete list of species (Fig. 2.2). Historical records were extracted from the literature, often assigned to broad time periods of one or two decades (e.g. 1940-60). Other types of card supplemented these species list cards: single-species cards, used for example when extracting records from museum collections, individual record cards for important finds such as first records of a species for a county, and general record cards (Marshall and Haes 1988).

Completed cards were archived at BRC, a total of a minimum of ca. 1,900 species-list cards, 900 single-species cards, 60 individual record cards, and 1,500 general record cards (numbers based on card types recorded in current scheme database). In order to process data and produce distribution maps, records were transcribed to machine-readable punched cards (ca. 3,100), and maps created with a mechanical plotter developed for publication of the first "Atlas of the British flora" (Perring and Walters 1962, Preston 2013).



ORTHOPTERA

LOCALITY

Date

V C No.

HABITAT

V C

Alt

Code No.

Grid Ref

Order No. 6426
ORTHOPTERA
(Grasshoppers, Crickets)

65 ACHETA	domestica
67 CHORTHIPPUS	albommarginatus
68	brunneus
69	parallelus
70	vagans
72 CONOCEPHALUS	discolor
73	darsalis
75 DECTICUS	verrucivorus
77 GOMPHOCERIPPUS	rufus
79 GRYLLOTALPA	gryllotalpa
81 GRYLLUS	campestris
83 LEPTOPHYES	punctatissima
85 MECONEMA	thalassinum
87 METRIOPTERA	brachyptera
88	roeselii
90 MOGOPLISTES	squamiger
92 MYRMELEOTETTIX	maculatus
94 NEMOBIUS	sylvestris
96 OMOCESTUS	rufipes
97	viridulus
99 PHOLIDOPTERA	griseoaptera
101 PLATYCLEIS	denticulata
103 STENOBOTHRUS	lineatus
104	stigmaticus
106 STETHOPHYMA	grossum
108 TACHYCINES	asynamorus
110 TETRIX	ceperoi
111	subulata
112	undulata
114 TETTIGONIA	viridissimo

Order No. 6428
DERMAPTERA
(Earwigs)

116 ANISOLABIS	annulipes
118 APTERYGIDA	albipennis
120 FORFICULA	auricularia
121	lesnei
123 LABIA	minor
125 LABIDURA	riparia
127 MARAVA	arachidis

Order No. 6420
DICTYOPTERA
Cockroaches

129 BLATTA	orientalis
131 BLATTELLA	germanica
133 ECTOBIUS	lapponicus
134	pallidus
135	panzeri
137 PERIPLANETA	americana
138	australasiae
140 PYCNOSCELUS	surinamensis
142 SUPELLA	supellectilium

Order No. 6425
PHASMIDA
(Stick-Insects)

144 ACANTHOXYLA	prasina
146 CARAUSIUS	morosus
148 CLITARCHUS	hookeri

BIOLOGICAL RECORDS CENTRE FEBRUARY 1968 RA4/B

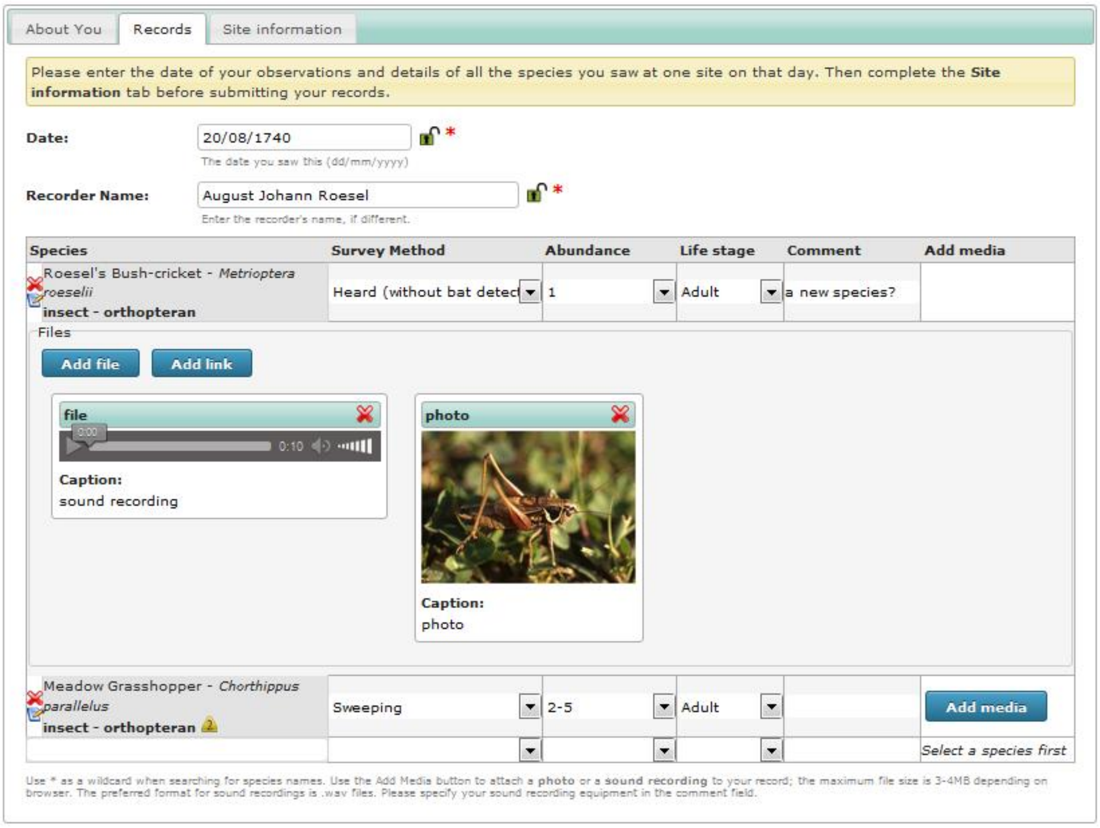
Fig. 2.2: Orthoptera Recording Scheme species-list recording card.

2.2.3.2 Digital systems

In 1974 BRC received access to a computer at Monks Wood research station for the first time. In order to handle and map records more efficiently, the essential details (species name, grid reference, year) began to be digitised, a time-consuming process which continued over many subsequent years across many species groups. With the spread of personal computers from the 1990s it became increasingly possible for individual recorders to digitise their own records. This led to a rapid increase in the number of computerised records, and in the amount of detail stored for each record: progressively more accurate dates, grid references and record attributes were stored, instead of the bare minimum needed for mapping (Preston et al. 2012).

2.2.3.3 Online recording

The development of the internet led to the next major change with the launch of online recording, allowing recorders to enter records directly into a central online database. A recording scheme website www.orthoptera.org.uk was created in 2008 at BRC with an online recording form, as well as species information. In the online form, date, species name, survey method, abundance, life stage and habitat are entered from drop-down lists of standard terms, and a spatial reference is set by clicking on a digital map which can be zoomed and viewed with a satellite image background, allowing precise pinpointing of the sighting. Digital photographs, and since 2015 digital sound files, can be attached directly to records to aid verification (Fig. 2.3).



Please enter the date of your observations and details of all the species you saw at one site on that day. Then complete the **Site information** tab before submitting your records.

Date: 20/08/1740 *
The date you saw this (dd/mm/yyyy)

Recorder Name: August Johann Roesel *
Enter the recorder's name, if different.

Species	Survey Method	Abundance	Life stage	Comment	Add media
Roesel's Bush-cricket - *Metrioptera roeselii* **insect - orthopteran**	Heard (without bat detec	1	Adult	a new species?	
Meadow Grasshopper - *Chorthippus parallelus* **insect - orthopteran**	Sweeping	2-5	Adult		Add media
					Select a species first

Caption:
sound recording

Caption:
photo

Use * as a wildcard when searching for species names. Use the Add Media button to attach a **photo** or a **sound recording** to your record; the maximum file size is 3-4MB depending on browser. The preferred format for sound recordings is .wav files. Please specify your sound recording equipment in the comment field.

Fig. 2.3: Orthoptera Recording Scheme online recording form.

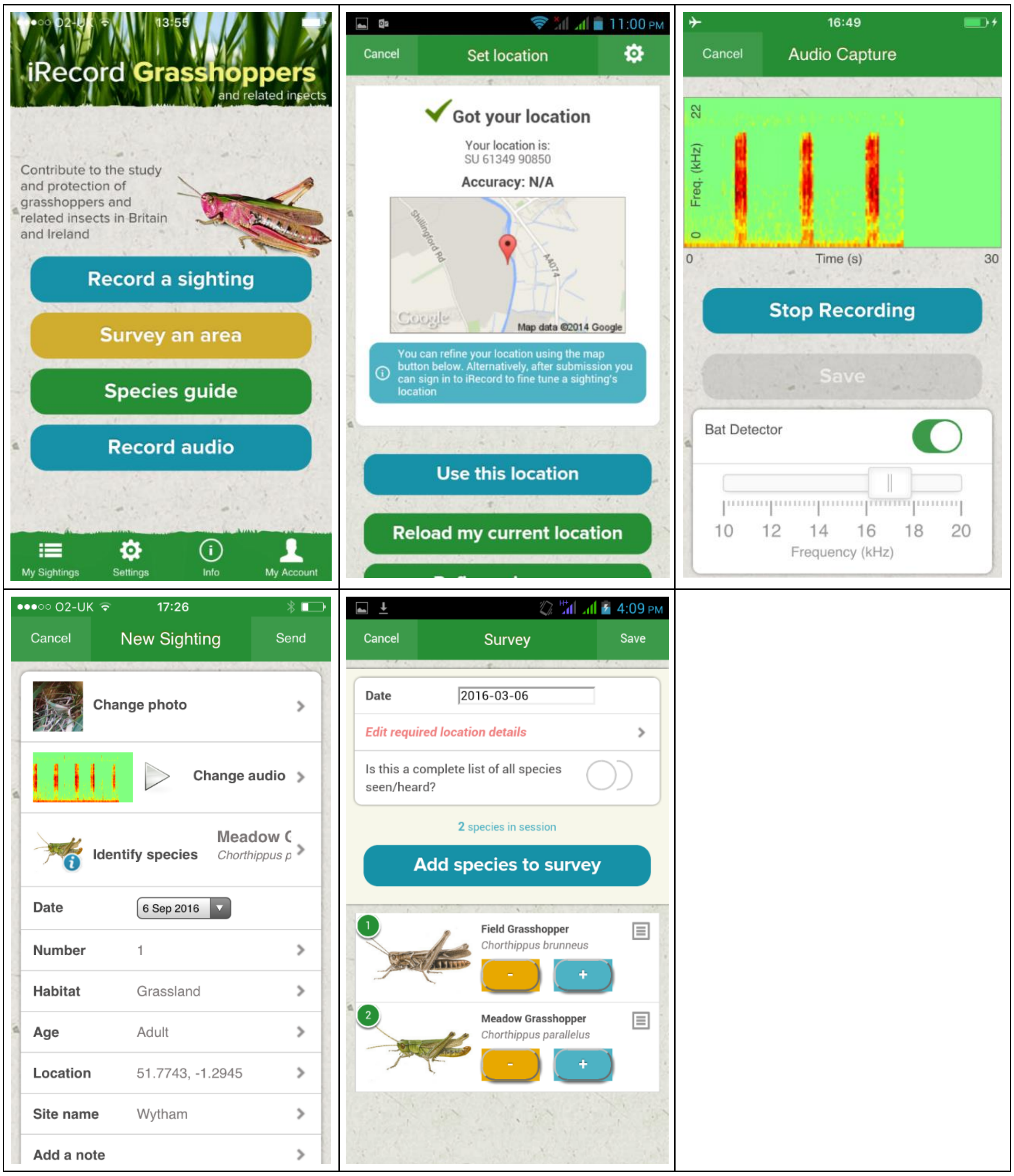
The form allows entry of a list of species for a field site with associated attributes, and sound recordings and photos to aid verification. It can be found at www.orthoptera.org.uk/survey.

The Orthoptera online recording form submits data to the "iRecord" system maintained by BRC, www.brc.ac.uk/irecord. Multiple other websites and surveys feed records into iRecord. Unless specified otherwise, records from all sources are available to the recording scheme to verify and use with appropriate acknowledgement.

The recording scheme also receives regular exports of data from another online recording system, "iSpot" www.ispotnature.org. iSpot was set up in 2009 and is aimed at users who are seeking help with species identifications from other users. iSpot records are verified prior to import into the recording scheme database based on associated photos and iSpot's user expertise scores.

2.2.3.4 Mobile app

The advent of mobile technology and the widespread use of smartphones (71% of adults in the UK owned a smartphone in early 2016 (Ofcom 2016)) have created an opportunity to provide species identification and record submission applications to recorders that are conveniently available “on the go”. A mobile app for the Orthoptera Recording Scheme, “iRecord Grasshoppers”, was released in August 2015, available free for Android and Apple devices. It allows submission of single- and multi-species sightings to the iRecord database. The spatial reference can be set from the phone’s network or GPS position, and / or using a digital map which can be zoomed and set to display a satellite image background. As with the online recording form, photos can be attached directly to records to aid verification. A significant update to the app in 2016 added sound recording functionality, allowing users to make 30-second uncompressed (.wav file format) sound recordings in the field with their phone and attach them to records. The update also includes a heterodyne “bat detector” function, which means that the mobile phone can make quiet and high-pitched Orthopteran calls up to ca. 22 kHz easier to hear. Records can be uploaded directly in the field or stored and uploaded later when internet connectivity is available (Fig. 2.4).



Contribute to the study and protection of grasshoppers and related insects in Britain and Ireland

Got your location

Your location is:
SU 61349 90850

Accuracy: N/A

You can refine your location using the map button below. Alternatively, after submission you can sign in to iRecord to fine tune a sighting's location

Bat Detector

Identify species Meadow C Chorthippus p

Date 6 Sep 2016

Number 1

Habitat Grassland

Age Adult

Location 51.7743, -1.2945

Site name Wytham

Add a note

Date 2016-03-06

Edit required location details

Is this a complete list of all species seen/heard?

2 species in session

1 Field Grasshopper *Chorthippus brunneus*

2 Meadow Grasshopper *Chorthippus parallelus*

Fig. 2.4: Screenshots of iRecord Grasshoppers app.

Screenshots of main menu, location setting, audio capture with "bat detector" function, and single- and multi-species recording.

2.2.4 Data flow and quality control

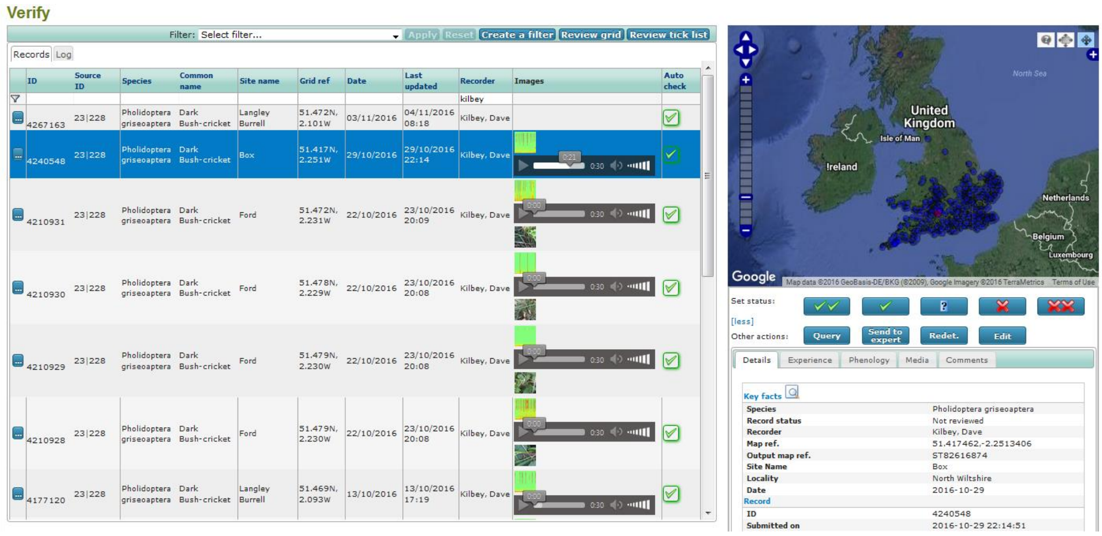
Quality control of records is an essential part of all recording schemes. Most records submitted to the Orthoptera recording scheme are of high quality in terms of species identifications and error rates have generally been low ((Marshall and Haes 1988), and see below). New technologies are encouraging a very welcome broadening of participation in recording and quality control is becoming increasingly important (Pocock et al. 2015b), not only for maintaining high data quality, but also as a valuable tool for providing feedback and developing the identification skills and longer-term support of a wider range of participants.

During the first decades of the recording scheme's operation, recording cards were sent out by BRC to recorders and completed cards returned via national or county recorders. Verification of records occurred through communication with recorders. Supporting evidence such as photographs and specimens could not be stored directly with records.

With the advent of personal computers, data flow from recorders to the scheme database could be conducted in digital formats throughout, with records sent by recorders to county or national coordinators, collated, processed and checked, and imported into the scheme database. Database programmes dedicated to biological recording such as "MapMate" and "Recorder" improved standardisation of records and allowed quick production of dot maps and interrogation of records, facilitating the verification process. They also allowed efficient record exchange between users of the same system through synchronisation protocols. Record exchange between systems, however, remains prone to introducing errors and record duplication, as it requires manual reformatting.

The development of online recording has allowed record submission, quality control and archiving all to be performed within one central database, which can be accessed by multiple users with different access permissions, reducing the need for data exchange between systems. Fig. 2.5 illustrates the iRecord verification system used by the Orthoptera Recording Scheme. Verifiers can review photos and sound recordings attached directly to records, and records are displayed in the context of others of the same species so that location and phenology can be easily compared. Automatic checks flag up records outside the expected distribution and season. Errors can be corrected directly, the recorder asked for additional information, or records forwarded to other experts. Once a conclusion is reached, verifiers assign one of five verification statuses: "correct", "considered correct", "plausible", "unable to verify" or "incorrect", with records in the first two categories accepted for further use. Currently six Orthoptera county recorders are verifying records in their counties, and the scheme is continuously aiming to get additional ones involved; records from remaining counties are verified by national coordinators (Table 2.2).

Out of 10,580 online records assessed by February 2017, the species name was changed for 186 and a further 41 were rejected altogether, implying an error rate in species identification of 2.2%.



ID	Source ID	Species	Common name	Site name	Grid ref	Date	Last updated	Recorder	Images	Auto check
								kilbey		
4267163	23|228	Pholidoptera griseoaptera	Dark Bush-cricket	Langley Burrell	51.472N, 2.101W	03/11/2016	04/11/2016 08:18	Kilbey, Dave		✓
4240548	23|228	Pholidoptera griseoaptera	Dark Bush-cricket	Box	51.417N, 2.251W	29/10/2016	29/10/2016 22:14	Kilbey, Dave	0:21 0:30	✓
4210931	23|228	Pholidoptera griseoaptera	Dark Bush-cricket	Ford	51.472N, 2.231W	22/10/2016	23/10/2016 20:09	Kilbey, Dave	0:00 0:30	✓
4210930	23|228	Pholidoptera griseoaptera	Dark Bush-cricket	Ford	51.478N, 2.229W	22/10/2016	23/10/2016 20:08	Kilbey, Dave	0:00 0:30	✓
4210929	23|228	Pholidoptera griseoaptera	Dark Bush-cricket	Ford	51.479N, 2.230W	22/10/2016	23/10/2016 20:08	Kilbey, Dave	0:00 0:30	✓
4210928	23|228	Pholidoptera griseoaptera	Dark Bush-cricket	Ford	51.479N, 2.230W	22/10/2016	23/10/2016 20:08	Kilbey, Dave	0:00 0:30	✓
4177120	23|228	Pholidoptera griseoaptera	Dark Bush-cricket	Langley Burrell	51.469N, 2.093W	13/10/2016	13/10/2016 17:19	Kilbey, Dave	0:00 0:30	✓

Key facts	
Species	Pholidoptera griseoaptera
Record status	Not reviewed
Recorder	Kilbey, Dave
Map ref.	51.417462,-2.2513406
Output map ref.	ST82616874
Site Name	Box
Locality	North Wiltshire
Date	2016-10-29
Record	
ID	4240548
Submitted on	2016-10-29 22:14:51

Fig. 2.5: Example screenshot of iRecord verification system.

Table 2.2: Numbers of verified Orthoptera records 2009-16

verifier	active since	county	no. of records verified
Hickman, Adrian	2016	Berks, Bucks, Oxon	27
Williams, David	2015	Shropshire	73
Carle, Ian	2015	Hertfordshire	97
Partridge, Rob	2014	Cambridgeshire	67
Hobbs, Ralph	2014	Sussex	521
Chesmore, Dave	2012	Yorkshire	227
Beckmann, Bjorn	2009	all counties	9,568

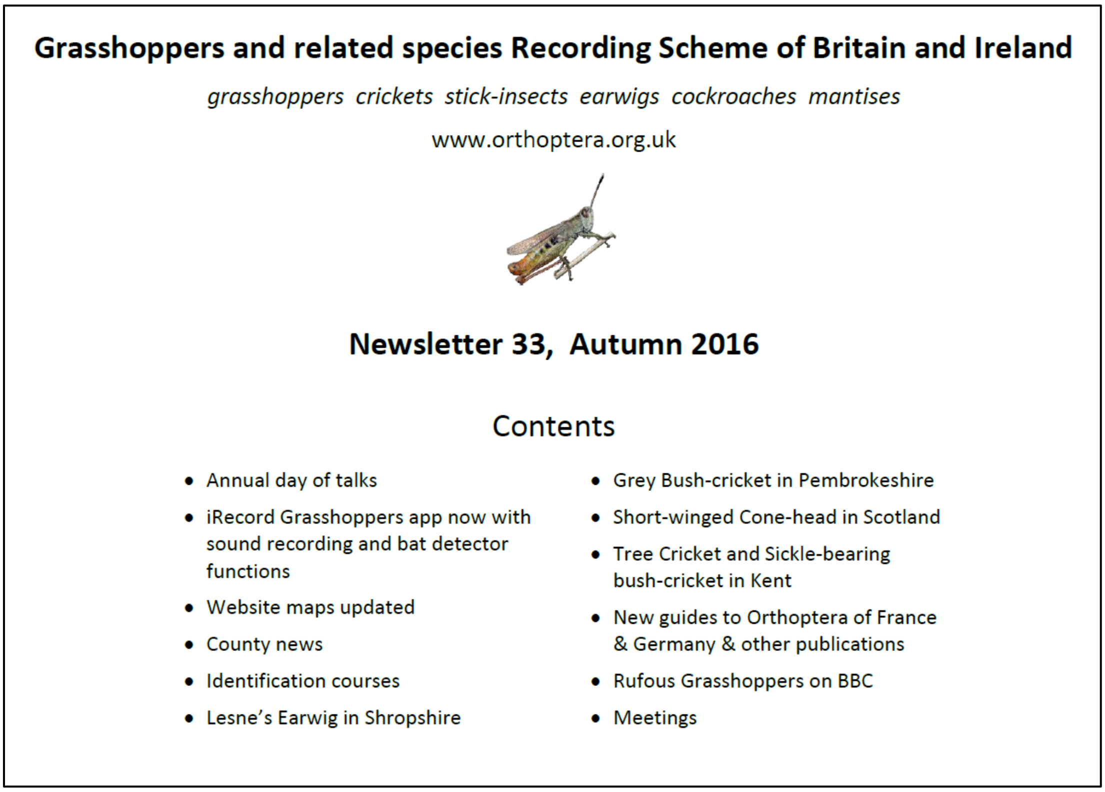
In 2001 the National Biodiversity Network Gateway was established in order to make records for all species groups and from many different providers publically available on the internet. The Gateway was replaced by the "NBN Atlas" (https://nbnatlas.org) in April 2017, which currently holds over 215 million records, including verified records from many national recording schemes such as the Orthoptera. Upload of verified records from iRecord is semi-automated, allowing it to occur more frequently than previously and thereby enhancing the visibility and accessibility of the data for research and conservation purposes.

2.2.5 Communication with recorders

Like other recording schemes, the Orthoptera scheme relies almost exclusively on volunteers for record collection, and their time, commitment and knowledge are critical to its operation. Effective feedback and communication with recorders are key to motivating, retaining and developing volunteers, and are among the top priorities for a recording scheme's success (Pocock et al. 2015a). Motivations of recorders are diverse and can change over time as participants become more experienced, and feedback should ideally aim to be of relevance to all – from novice recorders to taxonomic experts, and from casual observers to keen naturalists, scientists and conservation professionals (Isaac and Pocock 2015).

Direct communication with individual recorders through letters, or more recently emails, is the most personal and effective but also most time-consuming way of providing feedback. The iRecord online verification system has made this process more efficient, with a button opening up an email to the recorder containing the full record details (Fig. 2.5). In addition, recorders are automatically notified of verification decisions, so basic feedback is provided for every record at this point. A similar role is performed by a "Latest Images" section on the Orthoptera scheme website, where photographs appear once verified. The iRecord home page displays photographs of recently entered records, and registered users can explore records of all other users. The iRecord Grasshoppers app has an associated summary website displaying recent photos and league tables of recorders, species and counties.

More detailed and formal communication with recorders of the Orthoptera recording scheme occurs through scheme newsletters, which provide updates on results of recording activities, meetings, publications and other news (Haes 1979-1995, Widgery 1996-2002, Beckmann & Sutton 2013-2016, www.orthoptera.org.uk/newsletters) (Fig. 2.6). The "Wildlife reports" section of *British Wildlife* magazine provides similar feedback in a shorter format and at more frequent intervals, and it communicates the recording scheme's activities to a wider audience of naturalists (Haes 1990-1995; Widgery 1995-2002; Sutton 2002-2016; www.britishwildlife.com). County recorders and Local Record Centres often communicate with their networks of naturalists through local publications (e.g. www.rnhs.org.uk/old-copies-of-fieldfare).



Grasshoppers and related species Recording Scheme of Britain and Ireland

grasshoppers crickets stick-insects earwigs cockroaches mantises

www.orthoptera.org.uk

Newsletter 33, Autumn 2016

Contents

- Annual day of talks
- iRecord Grasshoppers app now with sound recording and bat detector functions
- Website maps updated
- County news
- Identification courses
- Lesne's Earwig in Shropshire
- Grey Bush-cricket in Pembrokeshire
- Short-winged Cone-head in Scotland
- Tree Cricket and Sickle-bearing bush-cricket in Kent
- New guides to Orthoptera of France & Germany & other publications
- Rufous Grasshoppers on BBC
- Meetings

Fig. 2.6: Front page of latest Orthoptera recording scheme newsletter (www.orthoptera.org.uk/newsletters).

Social media allows quick, public communication with recorders on the topics of the recording scheme, e.g. via Twitter (https://twitter.com/GrasshopperSpot) and Facebook (https://www.facebook.com/groups/1638188166466726), and helps to spread information about the recording scheme to new audiences. The Twitter feed is also displayed on the recording scheme website.

Occasionally opportunities arise for the recording scheme to feature in the broadcast and print media, and these can be valuable in increasing public awareness of the scheme's existence and recruiting new participants. For example, the scheme has recently received mentions on the BBC One Show, BBC Radio Oxford, the BBC website, the Times' 'weather eye' column and Country Life magazine.

Since 1980 the annual Orthoptera Special Interest Group meetings of the Royal Entomological Society have provided an opportunity for scheme recorders, scientists and others to meet and present or listen to talks about Orthoptera research (www.royensoc.co.uk/sig/orthoptera.htm).

2.2.6 Identification resources

2.2.6.1 Museum collections

Museum collections of specimens have traditionally provided the basis for descriptions and identification of species and continue to play an important role particularly in difficult cases where the taxonomy is not clear (Gorochov and Marshall 2001, Pinchen 2009). Collections may also be useful for identification courses. Important parts of many museum collections have been contributed by unpaid biological recorders (Miller-Rushing et al. 2012).

2.2.6.2 Field guides

For every-day use in the field and for a wider audience, accessible identification guides are a key resource, and they are among the top priorities for successful recording of a species group and can greatly enhance its profile (Preston et al. 2012, Pocock et al. 2015a). Over recent decades, publishing books has become cheaper and more flexible, and with increasing availability of high quality digital photographs identification guides have tended to become better illustrated and more accessible (Preston et al. 2012).

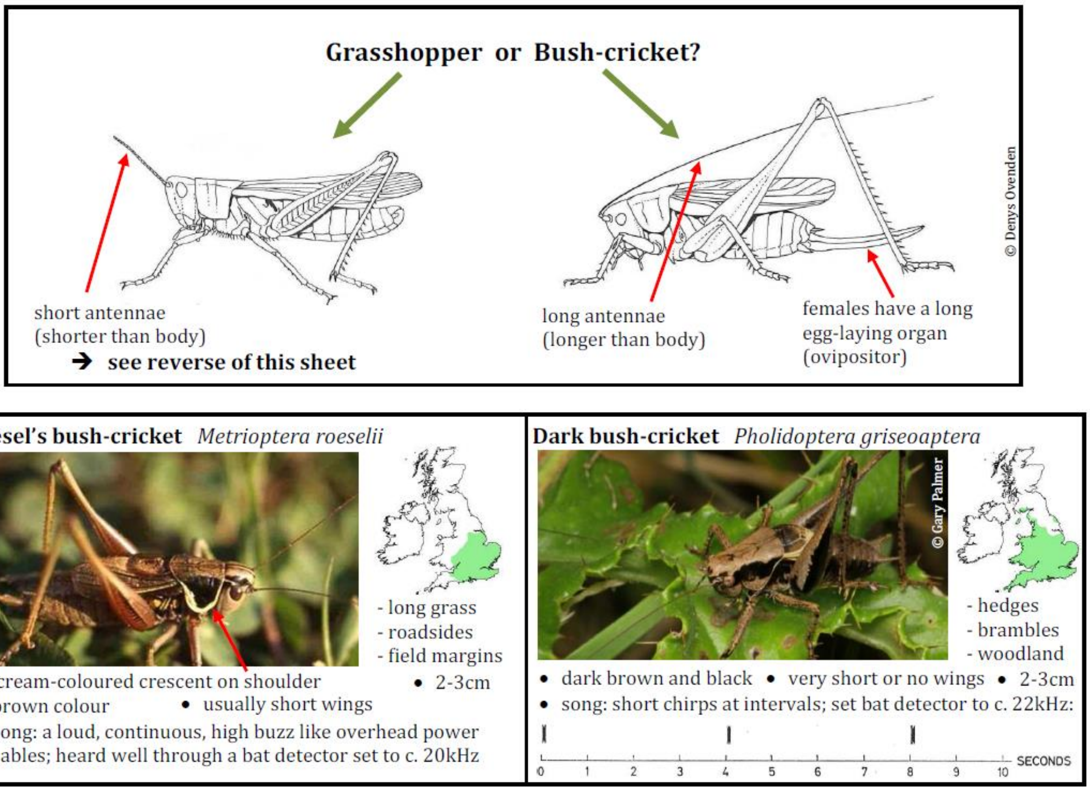
Important identification guides for British Orthoptera during the recording scheme’s operation have been: (Ragge 1965), with detailed species accounts, illustrations, song diagrams and county-level distribution maps; (Marshall and Haes 1988), with a dichotomous key, comprehensive species accounts, species illustrations and 10km grid square maps of current and historic distributions; (Evans and Edmondson 2007), providing the first full photographic key of the British and Irish species and comprehensively illustrating characteristics of males and females, adults and young, and different colour forms of all species; and (Benton 2012), covering species in greater detail than any of the previous publications, and containing a DVD with video clips illustrating songs, egg laying and other behaviour of most species.

For novice recorders, the fold-out chart of grasshoppers and related species published by the Field Studies Council in 1999 provides a convenient and inexpensive first identification guide (Marshall and Ovenden 1999).

2.2.6.3 Online resources

The internet has made free and instant access to identification guides possible, further increasing availability of information beyond specialist audiences. The Orthoptera recording scheme website provides short descriptions, a gallery of photographs and summary information on habitats and life history for each species (www.orthoptera.org.uk/species). In addition, the digital format allows convenient embedding of sound recordings directly on each species page; for most species, several calls are illustrated as heard with and without a bat detector.

To summarise identifications of common species in a convenient format, 2-page sheets covering grasshoppers, crickets, earwigs and cockroaches were put together in 2013 and made available on the scheme website for recorders to download and print (Fig. 2.7) (Beckmann 2013). These have proved useful to send out during online verification to first-time recorders, and to hand out as free copies during educational events.



Grasshopper or Bush-cricket?

short antennae
(shorter than body)
➔ **see reverse of this sheet**

long antennae
(longer than body)

females have a long
egg-laying organ
(ovipositor)

© Denys Ovenden

Roesel's bush-cricket *Metrioptera roeselii*

© Peter Sutton

- long grass
- roadsides
- field margins

- cream-coloured crescent on shoulder
- 2-3cm
- brown colour
- usually short wings
- song: a loud, continuous, high buzz like overhead power cables; heard well through a bat detector set to c. 20kHz

Dark bush-cricket *Pholidoptera griseoaptera*

© Gary Palmer

- hedges
- brambles
- woodland

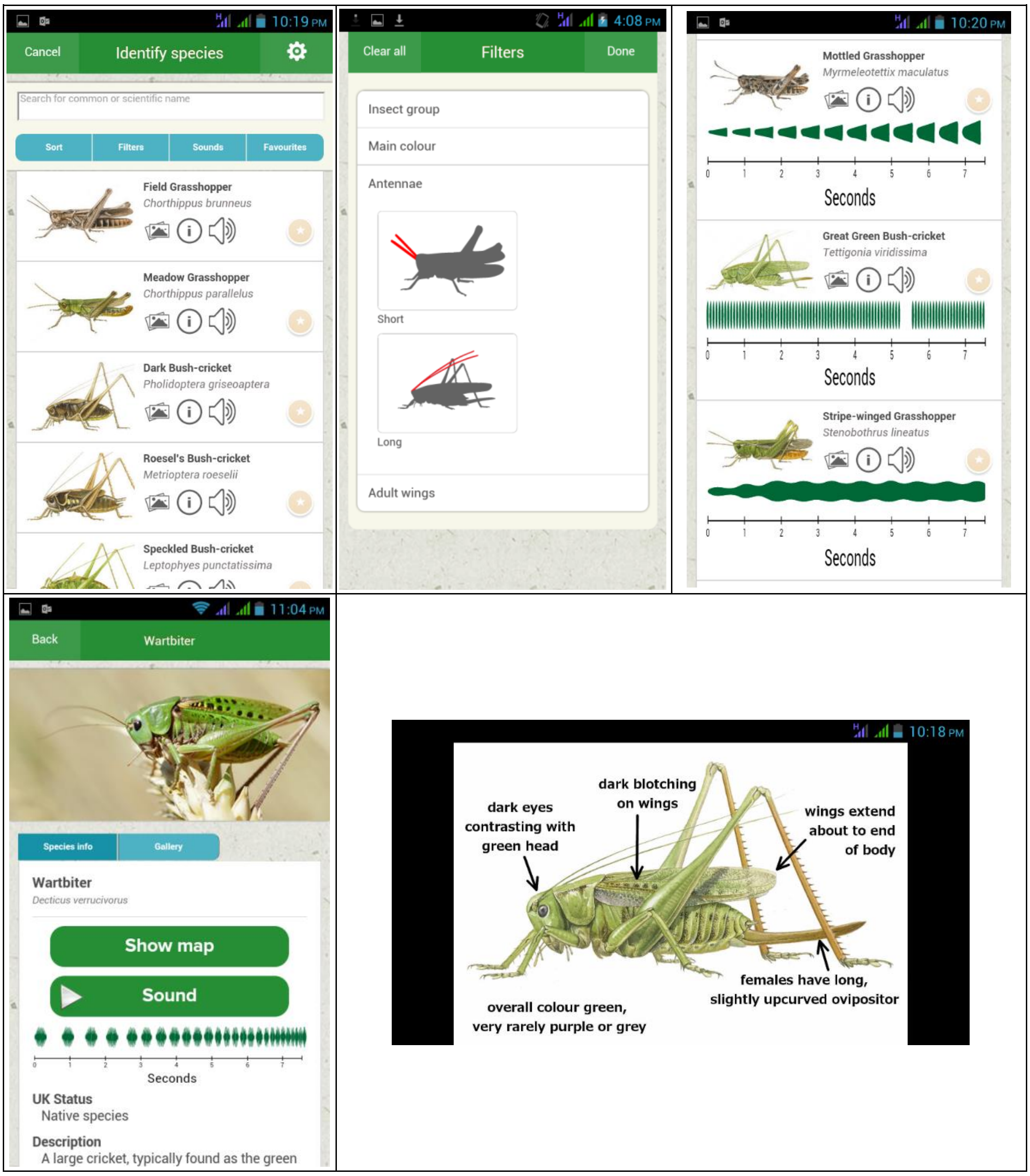
- dark brown and black
- very short or no wings
- 2-3cm
- song: short chirps at intervals; set bat detector to c. 22kHz:

Fig. 2.7: Head of identification sheet for common grasshoppers and crickets.
Guides are available for download on the Orthoptera recording scheme website www.orthoptera.org.uk/node/1035 (Beckmann 2013).

There is a growing number of other excellent online resources for species identification, for example, county-level guides such as for Worcestershire http://worcestershireorthoptera.weebly.com and Leicestershire www.naturespot.org.uk/taxonomy/term/19476), and annotated collections of macro-photographs such as Steven Falk's "Flickr" pages www.flickr.com/photos/63075200@N07/collections/72157631291968800.

2.2.6.4 Mobile app

Mobile technologies and the widespread use of smartphones mean that recorders can conveniently carry digital identification guides with them in the field. The iRecord Grasshoppers app comprises a field guide with species accounts, identification tips, photos, detailed labelled illustrations, and sound recordings. A set of descriptive filters including length of antennae, length of wings, colour and geographical region helps to narrow down the choice of species to aid identification. Species can also be filtered to those which produce sounds so that sound diagrams can be compared (Fig. 2.8).



A large cricket, typically found as the green

Fig. 2.8: Screenshots of iRecord Grasshoppers app showing field guide and species identification screens.

2.2.6.5 Bat detectors

The widespread availability of affordable "bat detectors" from the 1990s onwards has given Orthoptera recorders a useful tool for detecting high-pitched and quiet Orthoptera calls more easily. This applies particularly to two species of bush-cricket whose calls are mostly ultrasonic (Speckled Bush-cricket *Leptophyes punctatissima*, peak call energy at ca. 40 kHz, and Short-winged Conehead *Conocephalus dorsalis*, ca. 30 kHz). As of late 2016, the iRecord Grasshoppers app also includes a bat detector function, making this technical aid available for free to a wider range of recorders (Fig. 2.4).

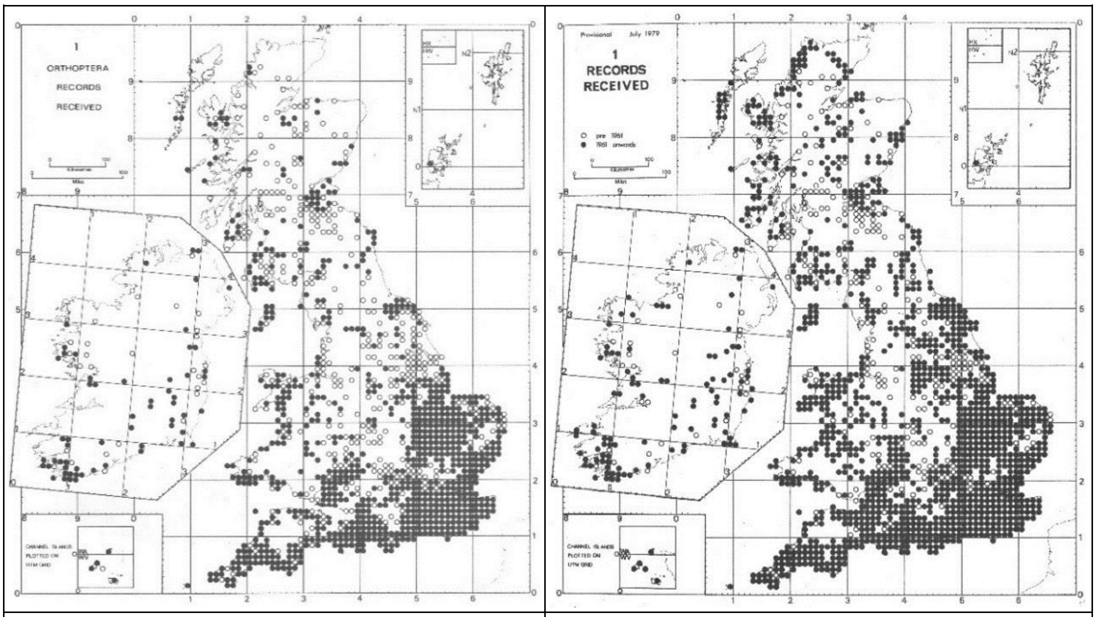
2.2.6.6 Identification courses

Practical identification courses provide an ideal way to learn about species and survey methods. A number of grasshopper and cricket identification courses are held annually, organised through the Field Studies Council, the Wildlife Trusts and other organisations (see www.orthoptera.org.uk/content/grasshopper-and-cricket-identification-courses-2016 for an example of 2016 courses). Course participants often go on to send in observations to the recording scheme.

2.2.7 Publications

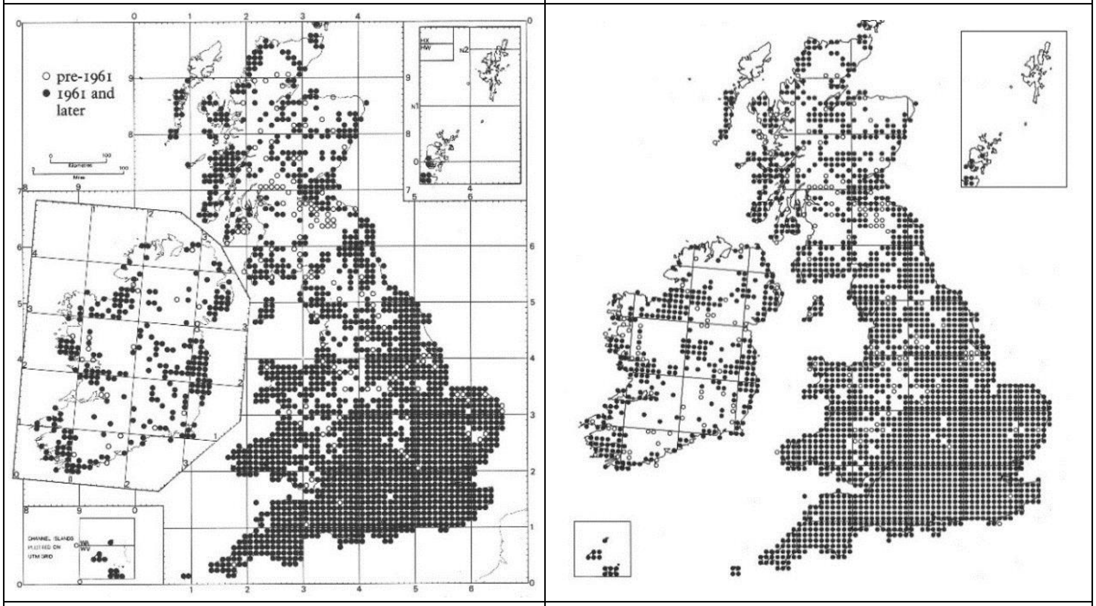
2.2.7.1 National Atlases

In parallel to many other national recording schemes, the primary publications of the Orthoptera scheme have been distribution atlases with 10km-square maps for each species (Roy et al. 2014). Atlases provide milestones of current knowledge of species distributions, and of changes in those distributions. They also serve to highlight remaining gaps in recording. Including three initial "provisional" atlases, the Orthoptera scheme has produced five national atlases to date (Skelton 1974, Skelton 1978, Haes 1979, Marshall and Haes 1988, Haes and Harding 1997). Fig. 2.9 illustrates the increasing geographical and taxonomic coverage of four of these atlases. The 1988 atlas was the first "non-provisional" one and a major publication, with detailed species accounts and extensive general chapters on Orthoptera and related species. A new atlas for the Orthoptera and allied insects of Britain and Ireland is in preparation for 2018, coinciding with the 50th anniversary of the establishment of the recording scheme. A set of draft atlas maps was appended to the spring 2013 scheme newsletter (www.orthoptera.org.uk/newsletters). The species accounts on the recording scheme website include dynamic distribution maps, which are coloured by year of most recent record, illustrating current database holdings.



1974: 1,196 hectads, 26 species mapped

1979: 1,576 hectads, 28 species mapped



1988: 2,099 hectads, 31 species mapped

1997: 2,423 hectads, 31 species mapped

Fig. 2.9: Recording coverage of four (provisional) Orthoptera atlases of Britain and Ireland. Maps reproduced from (Skelton 1974, Haes 1979, Marshall and Haes 1988, Haes and Harding 1997). Numbers of hectads and species are for Orthoptera only, excluding the related species groups.

2.2.7.2 County Atlases

As with other recording schemes, the Orthoptera scheme's activities helped to instigate the publication of county atlases, often compiled by county recorders and / or Local Environmental Record Centres (Preston et al. 2002). Many of these atlases aimed to map species distributions at finer resolutions than the 10km maps of national atlases, with 2km (tetrad) resolution being the most common. Thirty-four Orthoptera county atlases covering thirty Vice Counties have been published from the 1950s to the 2010s, with a further three currently in preparation (Figs. 2.10 & 2.11) (Beckmann 2017).

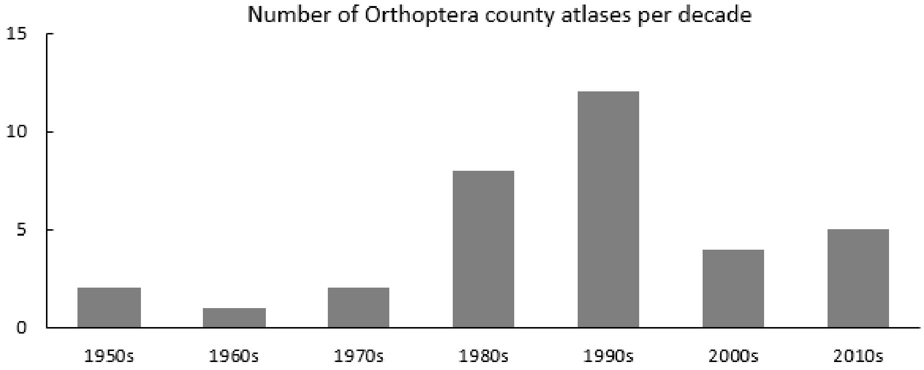


Fig. 2.10: Number of Orthoptera county atlases published, by decade.

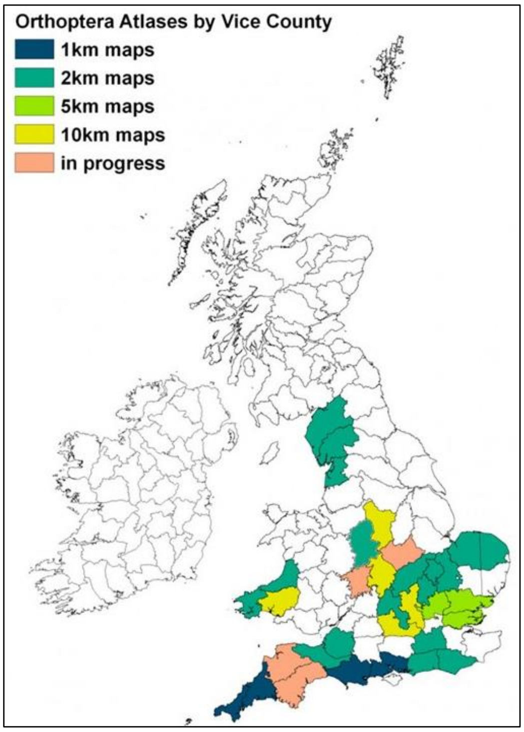


Fig. 2.11: Counties with Orthoptera atlases, and resolutions of maps.

For a full list see (Beckmann 2017).

2.2.7.3 Conservation status assessments

Apart from mapping species' distributions, assessing their conservation status has been a primary aim of recording schemes (Preston et al. 2012). At the most fundamental level, the data can document colonisations and extinctions of species: three colonisations of Orthopteran species have occurred in Britain since 2000 (cf. Table 2.1), and no extinctions are known to have occurred.

Between these extremes, assessments of species' threat status are of great interest for conservation, and status assessments of Orthoptera in Britain were published in 1987 and 2015, with six Orthopteran species assigned a threat status (Table 2.3) (Shirt 1987, Sutton 2015). Threat status assessments can have direct relevance to conservation action. For example, the rapid declines of the Wartbiter (*Decticus verrucivorus*) and Field Cricket (*Gryllus campestris*) documented by the recording scheme and corresponding threat statuses assigned in 1987 led to Biodiversity Action Plans for these species being drawn up, and captive breeding and reintroduction programmes being implemented, which are likely to have contributed to the persistence of these species in Britain, and a reduction in threat status of the latter species in the 2015 status review (Cherrill 1993, Edwards et al. 1996, Pearce-Kelly et al. 1998, Edwards 2008).

Table 2.3: Historical and current threat status assessments of Orthoptera in Britain

Species	**Shirt 1987**	**Sutton 2015**
Tettigoniidae		
Wartbiter *Decticus verrucivorus*	RDB2	EN
Gryllotalpidae		
Mole Cricket *Gryllotalpa gryllotalpa*	RDB1	CR
Gryllidae		
Field Cricket *Gryllus campestris*	RDB1	VU
Scaly Cricket *Pseudomogoplistes vicentae*	RDB1	VU
Acrididae		
Large Marsh Grasshopper *Stethophyma grossum*	RDB2	NT
Heath Grasshopper *Chorthippus vagans*	RDB3	NT

Old IUCN designations: RDB1 (Endangered), RDB2 (Vulnerable), RDB3 (Rare).

New IUCN designations: CR (Critically Endangered), EN (Endangered), VU (Vulnerable), NT (Near Threatened). Table adapted from (Sutton et al. in press).

While the original IUCN criteria for assigning threat status used in the 1987 assessment were defined without quantitative thresholds, a new set of criteria now stipulates the use of quantitative thresholds of geographic range size, and population size, trend, and degree of fluctuation, where these are available (Mace et al. 2008, IUCN 2012). The 2015 assessment judged threat status according to these new criteria, particularly range size and estimated population trend. The author emphasised that expert opinion was used in the interpretation of the recording scheme data, because they are unlikely to be comprehensive. The following sections assess the coverage and biases of the recording scheme data, and methods for distribution trend analysis.

2.3 Assessment of scheme data

Due to the evolution of the recording scheme and its methods of data collection reviewed above, records are not of a uniform quantity and quality over time. This section assesses the recording scheme's data holdings and associated biases. In light of this the subsequent section compares methods for distribution trend analysis. Both these sections focus on Britain only, as recording effort in Ireland is too sparse for detailed analysis at this time.

2.3.1 Record duplication

With the transfer of records between different software systems and different data custodians, records are frequently duplicated, as unique identification keys are not always transmitted, or reformatting is carried out in different ways at different times, for example recorder names stored with or without all initials. Duplication of records does not affect the production of distribution maps, but may need to be taken into account when calculating distribution trends, depending on the method of analysis used (see section 2.3 below). In order to avoid counting duplicate records, throughout this section "distinct records" were defined as unique combinations of species, grid reference and date. The total number of records for resident Orthopteran species in the scheme database is currently 126,368 (February 2017), compared to 104,237 "distinct records" for these species, suggesting that 17.5% of records are duplicates.

2.3.2 Change in number of records over time

In parallel with the recording scheme's growth since its establishment in 1968 and increasing ease of data computerisation there has been a large increase in the number of records submitted annually (Fig. 2.12): annual numbers of distinct records received have increased from several hundred in the 1960s and 70s to several thousand in the 1990s and 2000s. An early peak in record numbers in 1960 is due to historical records being assigned to the nearest decade (see section 2.1.3.1 above). An apparent decrease in numbers of records received since 2011 is likely to be due to lags in data flow from recorders, county recorders and Local Environmental Record Centres to the recording scheme database.

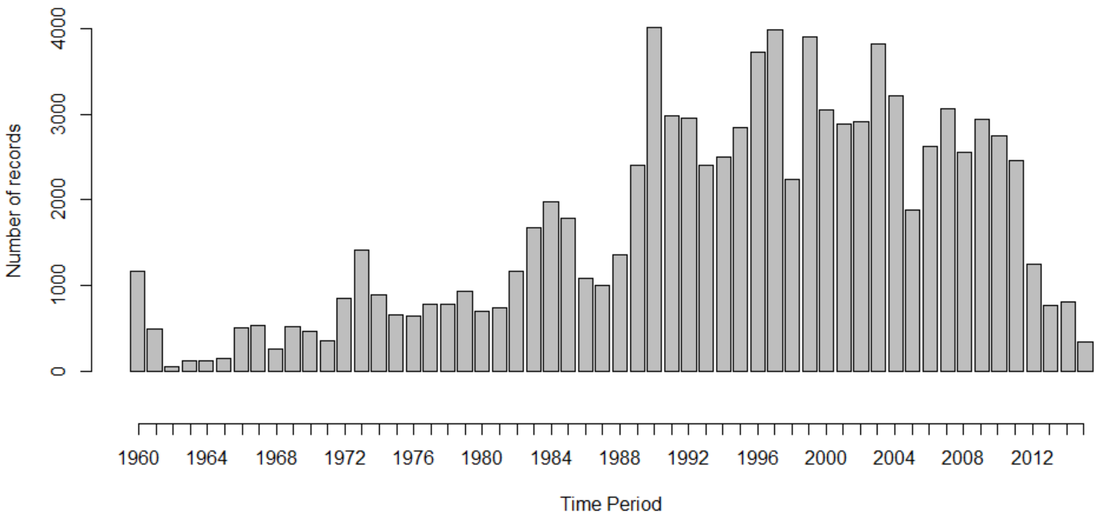


Fig. 2.12: Number of distinct records in Orthoptera Recording Scheme database by year of record, 1960-2015.

2.3.3 Geographical variation in recording

Over its history, the Orthoptera Recording Scheme has achieved fairly comprehensive coverage of Britain at a hectad level, but there is large spatial variation in recording intensity (Fig. 2.13): recording effort is highest in the south and east of Britain, with a strong northwards decline. Recording intensity therefore largely coincides with human population density, as well as Orthopteran species richness (cf. Fig. 2.1). There are some exceptions to this pattern, for example Cumbria and North Lancashire show a higher number of records than surrounding counties, even though human population density and Orthopteran species richness are not higher. These exceptions are likely to be mostly due to the strength of local recording networks and activities – for example Cumbria and North Lancashire have benefited from the presence of particularly active county recorders.

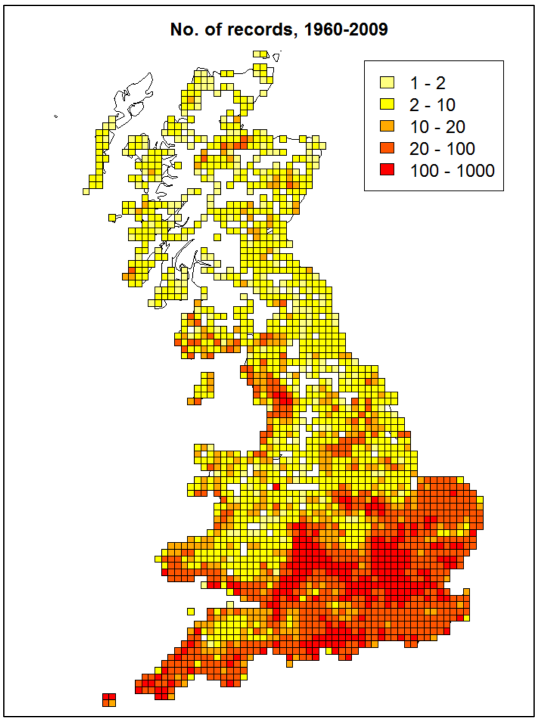


Fig. 2.13: Number of distinct records per hectad, 1960 to 2009.

Taken together, temporal and spatial variation in recording effort determine local changes in recording intensity. As an example, changes in recording effort per hectad were calculated over two time periods, 1960-2009 and 1980-2009 (Fig. 2.14): over the longer time period, there have been significant increases in recording effort in many areas, particularly the south-east of Britain, and few significant declines. Over the shorter time period greater regional differences are evident, with several significant regional declines as well as increases.

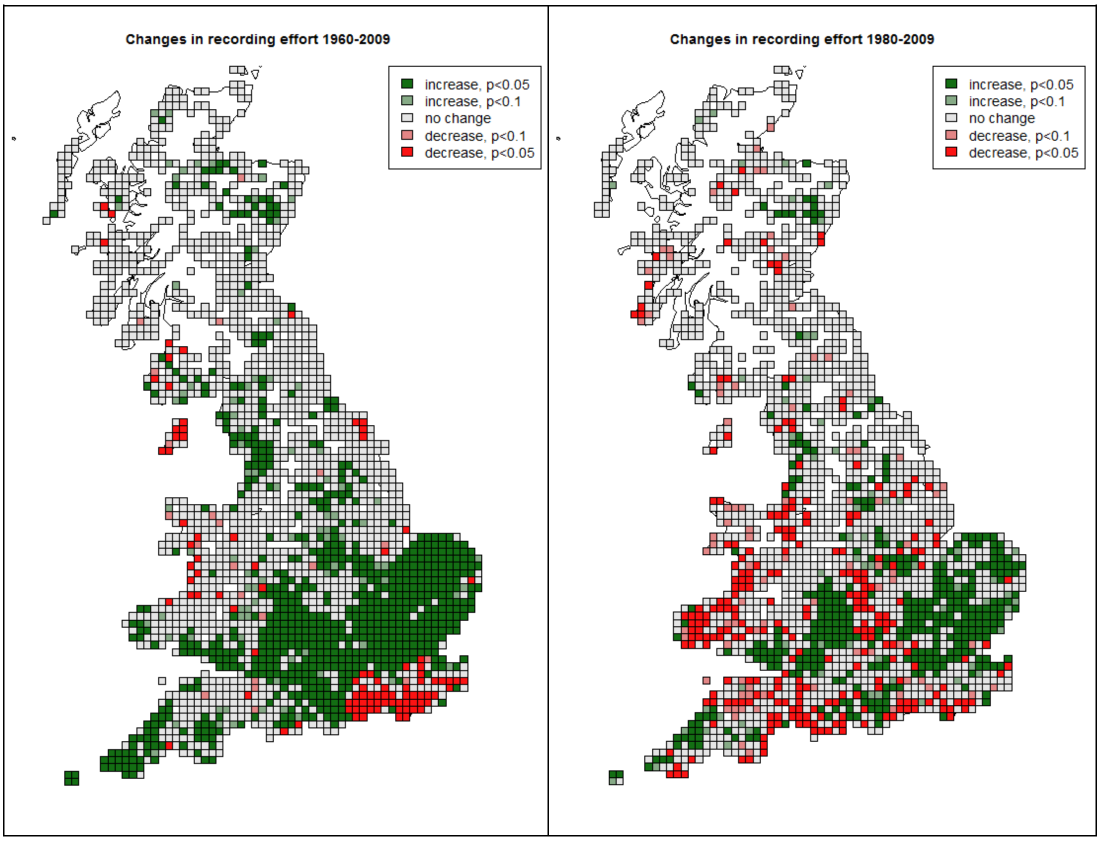


Fig. 2.14: Changes in recording effort per hectad 1960-2009 and 1980-2009. Changes were assessed by fitting Generalised Linear Models (GLMs) with a Poisson error structure to the annual number of distinct records per hectad over time in the Orthoptera recording scheme database. Colours indicate direction and significance of the relationship.

2.3.4 Spatial precision of records

While historically many early biological records in Britain were collected at a "Vice County" level, the 1962 "Atlas of the British flora" firmly established 10km grid squares as the precision level of choice for national distribution maps (Perring and Walters 1962, Preston 2013). Most recording of the Orthoptera scheme was initially focussed on this hectad precision, and until approximately 1980 the majority of records were collected at this resolution (Fig. 2.15). Recording at finer precisions of 1km and 100m squares steadily increased over time, including for the purposes of county atlases (Fig. 2.11) and due to increasing ease of digitisation (section 2.1.3.2). From about 1980 onwards more than 50% of records were collected at these resolutions, and by 1990 the proportion of records at only hectad resolution had declined to near zero. Since about 2010 the increasing use of online recording (Fig. 2.3) and the widespread availability of GPS devices, including in smart phones, has led to a sharp increase in even more accurate record localisations: 10m or 1m grid references had increased in number to about 30% of records in 2015, and this proportion is likely to increase further in future.

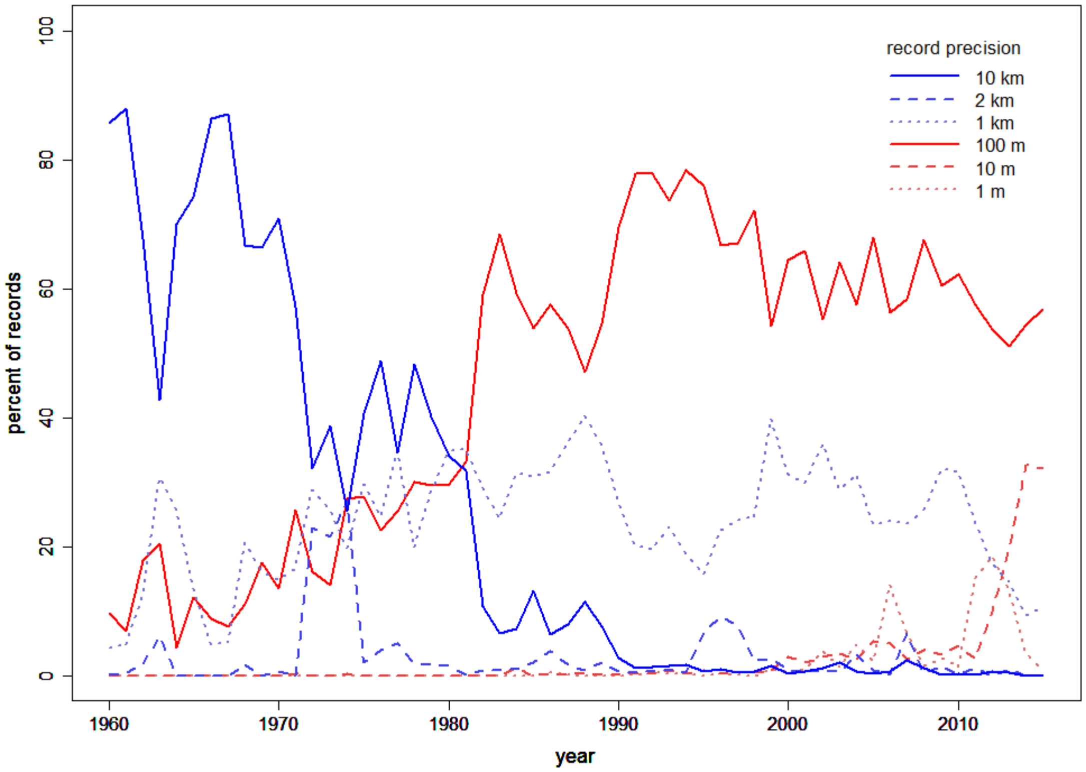


Fig. 2.15: Changes in the spatial precision of distinct Orthoptera Recording Scheme records over time.

2.3.5 Temporal precision of records

Until about 1970 a large majority of records in the Orthoptera recording scheme were dated with a temporal precision of a year, or a range of years (Fig. 2.16). Accuracy gradually increased, and while between 1970 and 1980 a majority of records were still specified to a year, a similar proportion were more precisely dated to a month. There was a further sharp increase in the temporal precision of recording from about 1980: by 1990 over 80% of record dates were specified as a day, and this proportion is now consistently near 100%.

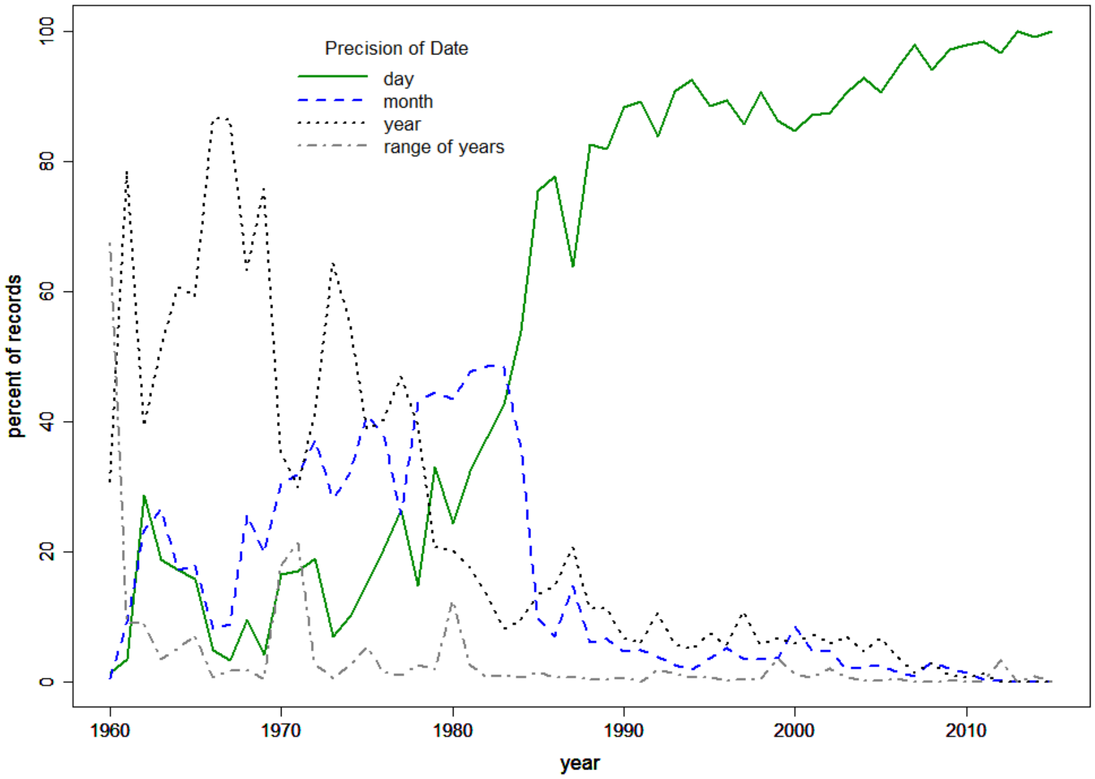


Fig. 2.16: Changes in the temporal precision of distinct Orthoptera Recording Scheme records over time.

The date of a small minority of records is specified to a range of days or months; these records are included in the day and month categories respectively.

2.3.6 Numbers of species recorded per visit

The number of species which a recorder logs on a visit to a site – also referred to as the "list length" – may naturally vary with site and date. It may also reflect the recording effort expended during that visit and is therefore used as an important parameter during data analysis (section 2.3): for example, a systematic search of a grid square by an experienced recorder is likely to result in a longer list than a casual search by a novice recorder.

Changes in list lengths in the Orthoptera recording scheme database were assessed by plotting them over time, and fitting generalised linear models (GLMs) with a Poisson error structure to list lengths over time, using the “dataDiagnostics” function in the R package “sparta”. Results showed that list lengths of distinct records as stored in the scheme database have declined significantly over time (Fig. 2.17a and Table 2.4a). However, as illustrated above (Figs. 2.15 & 2.16), the spatial and temporal precisions of recording and record notation have increased greatly over time, and there was no significant change in list lengths over time when only records of a minimum precision were considered and summarised at a fixed spatial resolution (here 1km – Fig. 2.17b and Table 2.4b).

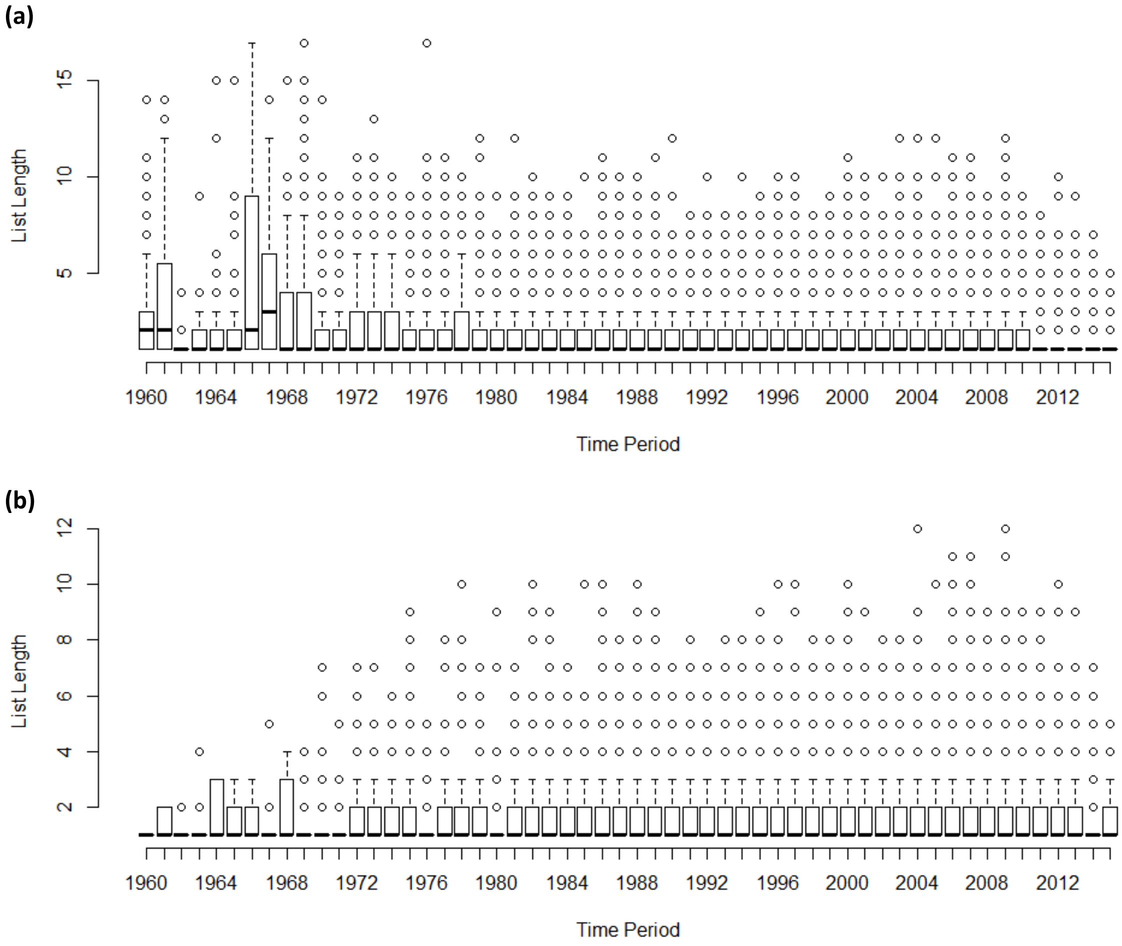


Fig. 2.17: Numbers of species recorded per visit (list lengths), 1960-2015.

Visits were defined as unique combinations of grid reference and date. Plots are based on records of all temporal and spatial resolutions (a), and records with a temporal precision of a day or month and a spatial resolution of 1km or finer only, summarised at a 1km square level for identical dates (b).

Table 2.4: Summary results of linear models of list lengths over time, 1960-2015.

		Estimate	**SE**	**t**	**P**	
(a) records of all spatial and temporal precisions	**(Intercept)**	0.72	7.74e-03	93.2	0.00	
	year	-2.3e-05	7.60e-07	-30.3	3.1e-201	***
(b) records with spatial precision of ≤ 1km and temporal precision of day or month, summarised at 1km	**(Intercept)**	0.52	1.12e-02	46.7	0.00	
	year	1.0e-06	1.03e-06	1.0	0.33	n.s.

2.3.7 “Presence-only” data

The Orthoptera scheme’s records are mostly gathered without any standard protocol or measure of recording effort. Even where recording is semi-systematic such as during a detailed survey of a site aimed at recording a complete species list for the purposes of a distribution atlas, no information is generally stored with the resulting records to indicate that they were part of such a survey, and species absences are not recorded. The multi-species recording form of the iRecord Grasshoppers mobile app does include the question “Is this a complete list of all species seen / heard?” with an associated tick box (Fig. 2.4), but this has received little use so far. As a result, almost all of the recording scheme’s data are “presence only” (i.e. detection only) data and there is no indication of whether a location without a record was surveyed for a particular species or not, with important implications for data analysis (see section 2.3 below).

2.3.8 Uneven detection

Uneven detectability of species is likely to result from changes in recorders’ skills over time, changes in the availability of recording tools such as identification guides and technical aids such as bat detectors, and detectability may also vary by habitat (Pellet et al. 2012, Isaac and Pocock 2015). Recorders choose which field survey methods to employ, for example visual or acoustic search, and what (if any) survey equipment to use, for example sweep nets or bat detectors. Survey methods and habitats can be recorded (Figs. 2.3 & 2.4), but this is not compulsory and currently happens for a minority of sightings only (survey method is recorded for about 6% of records, habitat for about 9%).

It is evident that changes in recording effort over time and space, changes in record notation, and the unstructured nature of recording generally, have entailed multiple changes and biases in the recording scheme data over time, which must be taken into account during analysis of a dataset of this kind. This is discussed in the next section, using distribution trend analysis as an example.

2.4 Distribution trend analysis

Once a recording scheme has established which species occur in a country and what their distributions are at a broad spatial scale, a next key question is whether these distributions are stable or changing over time. For example, distribution trends are an important criterion for assessing species' conservation status (IUCN 2012), and allow study of species' responses to environmental changes (chapters 3 and 4) (Powney and Isaac 2015).

It is clear that the nature and evolution of the Orthoptera recording scheme's methods of record collection and data transmission have led to a variety of biases in the data: uneven sampling both over time and space (Figs. 2.12-2.14), uneven spatial and temporal precision of recording and / or record notation (Figs. 2.15 & 2.16), uneven sampling effort per visit (Fig. 2.17), record duplication, and potentially uneven detectability of species. Distribution trend analyses of a dataset such as the Orthoptera recording scheme's therefore need to take these biases into account. The lack of absence (non-detection) records prohibits the use of conventional site-occupancy models for distribution trend analyses (MacKenzie et al. 2002), and some methods used for analysis of recording scheme data therefore infer absences in other ways.

As an example, three methods for distribution trend analysis were applied to the Orthoptera recording scheme data here over the 30-year time period 1980 to 2009. The performance of these methods was assessed previously in a study using simulated data (Isaac et al. 2014). In the discussion, the authors note that "Ultimately, the robustness of any model is dependent on its assumptions, and whether those assumptions are valid. We modelled a suite of recording scenarios, but there is a gap between our idealized simulations and the reality of how opportunistic data is collected." The purpose of this section is to (i) spell out clearly what assumptions are made by each method and (ii) how biases in the recording data are addressed. The aim is then (iii) to elucidate how analyses are best set up in order to meet the assumptions made and address the biases of a real-world dataset such as the Orthoptera recording scheme's. In addition, the section aims to (iv) investigate how similar the results of different methods are, and (v) what species, questions and purposes each method is most suitable for. Calculations were carried out in the statistical software environment "R" (R Core Team 2016) using the package "sparta", which was created at BRC to allow easy application of a number of trend analyses to unstructured recording data (August 2015, August et al. 2015b).

2.4.1 Relative range change index

2.4.1.1 Definition, calculation, outputs

The “relative range change index” is defined as change in the proportion of squares occupied by a species between two time periods relative to the overall change for all species of the taxonomic group (Telfer et al. 2002). Species occupying very few squares in the first time period (fewer than 5 squares being the recommended minimum) are excluded, because changes in these rarest species may affect results disproportionately. Only squares surveyed in both time periods are included in the analysis, by default defined as squares with at least one record for the taxonomic group in both time periods. Species ranges in each time period are expressed as proportions occupied of the total number of these surveyed squares, and logit-transformed. A linear model is then fitted to the species ranges in the later time period vs. the earlier time period, representing mean change in recording effort for all species. The standardised residual from this line for each species is defined as its relative range change index (Fig. 2.18). The index is therefore a single, relative value of range change per species, without a measure of significance for individual species. The index was here calculated between the 1980s and 2000s (Fig. 2.20, S 2.1 Table).

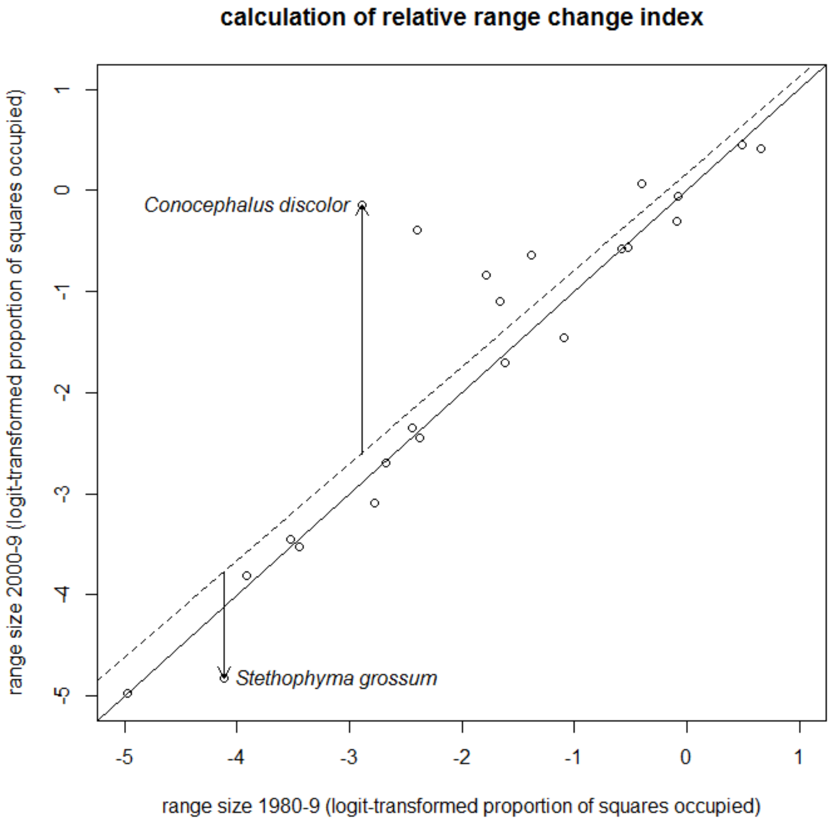


Fig. 2.18: Species' range sizes in 1980-9 and 2000-9 and calculation of relative range change index.

Range sizes are plotted as logit-transformed proportions of 10km squares occupied. The solid line indicates unity, i.e. equal range sizes in both time periods. The dashed line indicates a linear model, i.e. mean recorded range change across all species. The "relative range change index" is defined as change in range size relative to this mean, i.e. as the (standardised) residual distances from the regression line. Arrows illustrate residuals for the species with the greatest positive and negative range changes.

2.4.1.2 Meeting assumptions and addressing biases

The relative range change index assumes that recorders aim to record as many species of the taxonomic group per grid square as they can during each time period. Records should therefore be summarised at temporal and spatial scales at which the data collection process is likely to meet this assumption – for a national analysis this typically means hectad level spatial scale and many years per time period, i.e. the scales adopted by most national atlases (Telfer et al. 2002). Here, records were summarised at a 10km square and decade level (1980-9, 2000-9).

When records are summarised at these very large scales, uneven spatial and temporal precision of recording and / or record notation, and uneven sampling effort per visit, are not expected to overly affect results. Uneven detectability of species is also likely to be averaged out through the summarising of data at large spatial and temporal scales, and only if species regularly go undetected over many years and at all sites within hectads will results be affected.

Uneven spatial sampling is addressed by calculating change based on squares surveyed in both time periods only. By default these squares are defined as those with at least one record for the species group in each time period, but this threshold could be increased in order to restrict analysis to well-surveyed squares (Telfer et al. 2002) (cf. chapter 3).

The index addresses uneven sampling over time by defining range change relative to mean change: in the Orthoptera recording scheme, overall recording effort was higher in 2000-9 than in 1980-9 (cf. Fig. 2.12), with 5,160 unique species-hectad combinations in surveyed squares in 2000-9, compared to 4,228 in 1980-9. This is reflected in the linear model (dashed line in Fig. 2.18) having an intercept greater than zero and lying above the (solid) unity line. Accordingly, species recorded as occupying the same proportion of squares in both time periods (i.e. plotted on the unity line in Fig. 2.18) have a negative range change index and are judged to have declined relative to the mean.

Calculation of the range change index also assumes that there are no changes in the recording of particular species between time periods (Telfer et al. 2002). Data from targeted surveys of individual species conducted in one time period only should therefore be excluded from analysis. For Orthoptera, targeted surveys were carried out for the Biodiversity Action Plan species, Wartbiter (*Decticus verrucivorus*) and Field cricket (*Gryllus campestris*) (Cherrill 1993, Edwards et al. 1996). In the present analysis, these species were excluded on the basis of rarity already (occupying less than 5 hectads in the 1980s). A potential change in recording of particular species may be due to the increasing availability of bat detectors, which may selectively increase recording of species that stridulate at high frequencies. In Britain, this particularly applies to the Speckled bush-cricket (*Leptophyes punctatissima*) and Short-winged conehead (*Conocephalus dorsalis*) (section 2.1.6.5). However, both species are also commonly observed by sight (Evans and Edmondson 2007, Benton 2012, Mearns and Marquiss 2016) and, summarised at coarse scales, their distributions are unlikely to be under-recorded even without the widespread use of bat detectors so in the present analysis this is not considered problematic.

2.4.1.3 Assessment and recommendations

While the design of the range change index and summarising of data at large spatial and temporal scales makes this method robust to several biases, it also makes it conservative, i.e. reduces its statistical power to detect change (Isaac et al. 2014). Power to detect negative trends in widespread species may be particularly low, because these are likely to have several populations per hectad (100km^2) which may not all disappear in close temporal proximity. Individual species' index values lack a measure of certainty, and their meaning is not easily conveyed to a non-scientific audience (the difference from the average change in proportion of squares occupied, on the logit scale), and may not be ideal for providing feedback to recorders for example. However, the method is suitable for conservative, relative assessments of species trends at large scales, particularly where as many species of a group as possible are to be compared, including those with limited numbers of records and records at low spatial and temporal resolutions.

2.4.2 Reporting rate models

2.4.2.1 Definition, calculation, outputs

“Reporting rate” methods calculate distribution trends as change in the annual proportion of visits which produce a record of a species, modelled as change over time in the probability of detection on the average visit, using logistic generalised linear mixed models (GLMMs). A random effect of site and a fixed effect of list length were added here to allow for variation by site and number of species recorded during visits (Isaac et al. 2014). The output is a single value per species of mean annual change over the study period in the proportion of visits during which it is detected, with a standard error, allowing assessment of significance (Fig. 2.20, S 2.1 Table).

2.4.2.2 Meeting assumptions and addressing biases

Reporting rate methods assume that recorders record species against a full list of the taxonomic group, i.e. that they search a site for all species and record all species they find. If a species is not recorded during a visit, therefore, the recorder is assumed to have looked for, but failed to find it. In this way, non-detections of species are inferred from detections of other species.

In the absence of explicit information in the database of which records meet the assumption of the recorder having recorded against a full list (section 2.2.7), several steps were taken in the selection of records and the setup of the analysis in order to increase the likelihood of this assumption being met. Firstly, data were analysed at the spatial and temporal resolution of a typical visit – here chosen to be 1x1km squares and 1 day – and records at coarser resolutions were discarded. Secondly, only records which occur on “lists” of a length of at least 2, and from sites sampled in at least 2 years during the study period were used and all others were assumed to be “casual” records not meeting this assumption and were discarded; “lists” were defined as the distinct species recorded during a visit, i.e. distinct species for the same day and 1km square (Isaac et al. 2014). Thirdly, only records for species were analysed together which are broadly similar in their ecology and phenology and are therefore likely to be recorded together. Here, only resident Orthopteran species of outdoor terrestrial habitats were selected. In addition, records for the winter months December to March were excluded, since no Orthopteran species other than groundhoppers (Tetrigidae) are regularly encountered during these months and winter records therefore cannot be considered full lists.

Records were summarised at the 1km resolution chosen for analysis in order to counteract uneven spatial and temporal precision of recording and / or record notation over time, which might bias list lengths (Figs. 2.15-2.17).

Records selected and summarised in these ways are referred to as “suitable” records in the following.

Covariates for site and list length were included in models because this has been shown to significantly improve handling of bias due to uneven spatial sampling and uneven sampling effort per visit, reducing type-1 errors (false positives, i.e. erroneous findings that a species’ probability of detection has changed over time when it has not) (Isaac et al. 2014). The list length variable is assumed to reflect recording effort during a visit, with an expectation of greater probabilities of detection during visits with greater list lengths. The results of the present analysis bear this out, with a significant positive effect of list length for all species (S 2.1 Table).

Reporting rate methods do not explicitly address bias due to changing detectability of species, and are liable to produce type-1 errors where data is biased in this way, and caution is needed where this may be the case (Isaac et al. 2014).

The decline estimated by the reporting rate model for the Heath Grasshopper *Chorthippus vagans* is much greater than for any other species, and highly significant; similarly, the positive effect for list length for this species is much greater than for any other species (Fig. 2.20, S 2.1 Table). While *C. vagans* does seem to have undergone declines over this period, and threat status assessments in 1987 and 2015 assigned it to categories “Rare” and “Near Threatened” respectively (section 2.1.7.3), the magnitude of the decline estimated by the model seems excessive compared to other species (Shirt 1987, Benton 2012, Sutton 2015). A likely explanation is that the number of positive “suitable” records available for analysis for *C. vagans* here was extremely low (24 records in 30 years), increasing the likelihood of such an extreme result arising by chance.

2.4.2.3 Assessment and recommendations

Reporting rate models are robust to several biases, and have greater statistical power to detect changes than the relative range change index (Isaac et al. 2014) and have been used, for example, to produce priority species indicators (Eaton et al. 2015). The models are fairly quick to fit, and produce absolute distribution trend values for each species that can be easily interpreted and communicated: mean change over the study period in the proportion of visits during which a species is detected. Associated estimates of error allow assessment of significance.

However, care is needed in the selection of species and records for analysis in order to ensure that the assumptions of species being recorded as complete lists per visit, and no changes in detectability occurring over time, are likely to be met. This will often mean that the majority of records is discarded, making the method suitable only for species with reasonably high quantity and quality of data: the extreme trend estimate for *C. vagans* highlights the importance of assessing robustness of results not by their significance alone, but also by the numbers of records used, which was extremely low in this case. A recent analysis of data of the UK Ladybird Survey, which employed reporting rate models, excluded all species with fewer than 1,000 “suitable” records (Roy et al. 2012). Even applying a less stringent cut-off of 500 “suitable” records to the Orthoptera Recording Scheme data here, this restriction still makes the method suitable for only 12 out of 23 species (Fig. 2.20, S 2.1 Table).

2.4.3 Occupancy-detection models

2.4.3.1 Definition, calculation, outputs

Occupancy-detection models are similar to the reporting rate models described above, but include an additional nested submodel for detection (MacKenzie et al. 2002, Tyre et al. 2003, Isaac et al. 2014). The probability of a site being occupied by a species, and the probability of the species being detected given that a site is occupied, are estimated separately in hierarchically coupled models in a Bayesian framework. A random effect for site was included in the state (presence-absence) model, and a fixed effect for list length in the observation (detection-nondetection) model in order to account for uneven spatial sampling and uneven sampling effort per visit.

The models produce absolute estimates of occupancy per species for each year of the study period, with credible intervals (Fig. 2.19). A trend over the entire study period can be derived from the yearly occupancy estimates, for example by calculating the difference in occupancy between the first and last study year. However, in species with large fluctuations in occupancy estimates from year to year, this approach is liable to produce different results depending on the exact choice of start- and end-year. A method less prone to this variability is fitting a model to the annual occupancy estimates, weighted by the inverse of their dispersions, i.e. giving less weight to years with greater uncertainty around the occupancy estimate. The sparta package currently does not produce such an overall trend estimate, so it was calculated here by fitting quasibinomial Generalised Linear Models to the mean annual occupancy estimates, weighted by the inverse of their coefficients of variation (Fig. 2.19, S 2.1 Table).

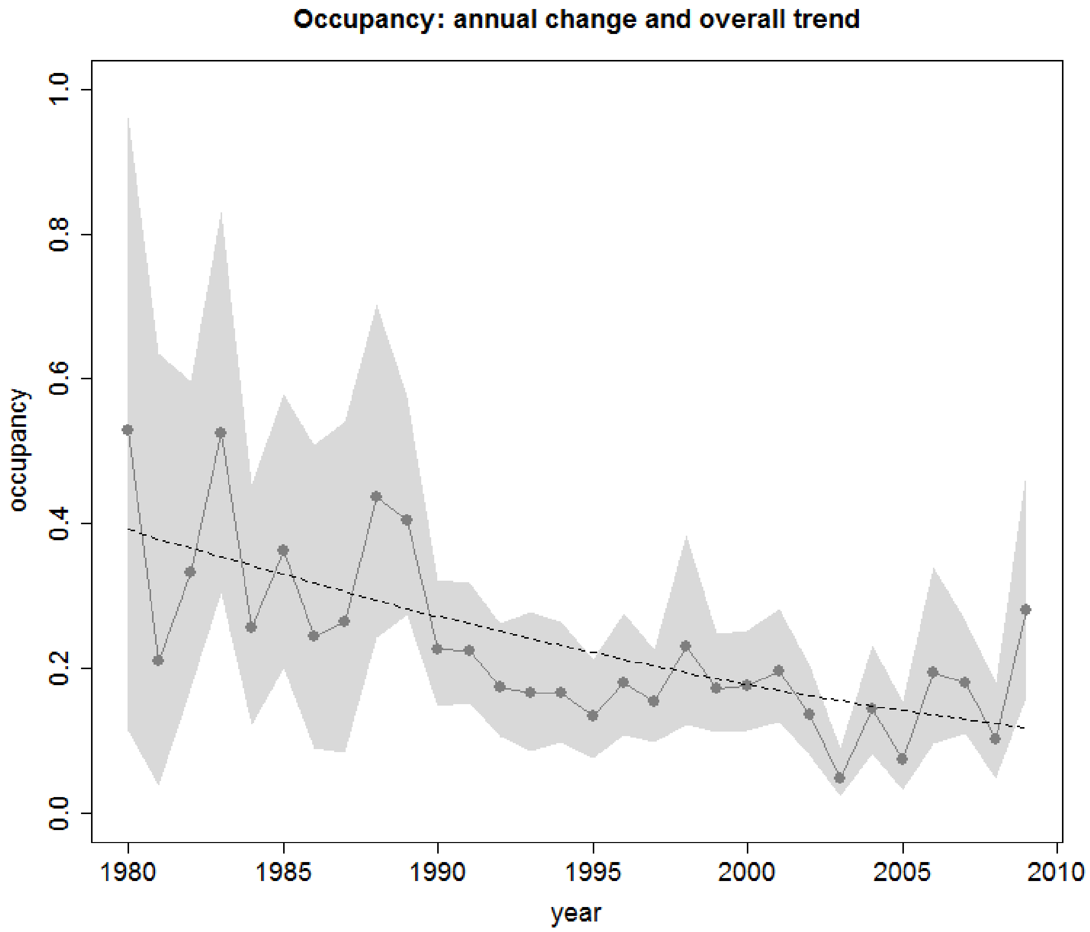


Fig. 2.19: Modelled annual occupancy and overall trend 1980-2009, for the Mottled Grasshopper *Myrmeleotettix maculatus*.

Points are mean annual estimates of occupancy, grey shading indicates 95% credible intervals. The dashed line indicates mean trend in occupancy over the study period.

2.4.3.2 Meeting assumptions and addressing biases

As with reporting rate models, occupancy detection models assume that recorders survey sites against a full list of species of the taxonomic group. The same steps as with those models were therefore taken in the selection of records and in the setup of the analysis to increase the likelihood of this assumption being met (section 2.3.2.2).

Estimating detection probability separately requires repeat observations in "closure" periods during which there is assumed to be no change in occupancy, i.e. no extinction or colonisation (Kéry and Schaub 2012). Closure periods were here defined as years, i.e. sites were assumed to remain occupied or not throughout each year, and changes in occupancy to occur only between years. Models could therefore only be fitted for species which have at least one site with repeat observations during the same year; all species analysed here had such sites. The steps taken to ensure records are likely to be part of a full list (section 2.3.2.2) were also assumed to suffice to meet the assumption of no changes in occupancy occurring within a year. Additional measures could theoretically be taken, for example the months analysed could be restricted further in order to focus even more tightly on the main phenological period of all species, increasing the likelihood of repeat visits encountering all species present. Alternatively, closure periods could be shortened, for example defined as months. However, any such measures would further reduce the numbers of available records.

2.4.3.3 Assessment and recommendations

Occupancy detection models with covariates of site and list length and site filtering were found to be generally very robust to biases and had good statistical power to detect change (Isaac et al. 2014). They provide annual absolute measures of occupancy (and derived from these, changes in occupancy over the study period), which are easily interpreted and communicated. For example, Fig. 2.19 illustrates that occupancy of the Mottled Grasshopper *Myrmeleotettix maculatus* is estimated to have declined from about 40% to less than 20% between 1980 and 2009, with greater certainty about the estimates after 1990 than before. As with reporting rate models, care needs to be taken in the selection of records and the setup of the analysis so that the assumptions of recording against a full list of species, and no changes in occupancy in closure periods, are likely to be met. Occupancy detection models have become the current method of choice for trend analysis of unstructured biological recording data (Hayhow et al. 2016), but are time-consuming to fit and, like reporting rate models, currently suitable only for species with a high quantity and quality of data. A recent study used a cut-off of a minimum of 500 suitable records per species (Woodcock et al. 2016).

2.4.4 Comparison of trend estimates

The distribution trend estimates for Orthoptera in Britain between 1980 and 2009 produced by the three methods – relative range change index, reporting rate and occupancy detection models – are compared in Fig. 2.20 and full results are given in S 2.1 Table. To assess the level of agreement between methods, results of trend measures were plotted against each other in pairs, and linear models fitted (Table 2.5, S 2.1 Fig.). The pairwise comparisons were carried out for all species, and for those twelve species only which had a minimum of 500 "suitable" records for reporting rate and occupancy models, in order to exclude species liable to produce unreliable estimates, particularly here *C. vagans* (cf. sections 2.3.2.3 and 2.3.3.3).

Pairwise comparisons of methods showed low to moderate agreement between reporting rate models and the two other measures when all species were included (R^2 values of 41% and 14%), but good agreement when species with fewer than 500 "suitable" records were excluded (R^2 values of 94% and 75%). There was fairly good agreement between the relative range change index and occupancy models for all species (R^2 65%), and this also improved slightly when species with few records were excluded (R^2 73%) (Table 2.5, S 2.1 Fig.).

Table 2.5: Coefficients of determination (R^2 values) of linear models for pairwise comparisons of trend measures

	Relative range change index vs. Reporting rate	**Occupancy detection vs. Reporting rate**	**Relative range change index vs. Occupancy detection**
all species (n=23)	0.41	0.14	0.65
species with >500 "suitable" records (n=12)	0.94	0.75	0.73

Models were fitted for all species (top), and for twelve species with a minimum of 500 "suitable" records for reporting rate and occupancy models (bottom). Results show the level of agreement between distribution trend measures (for R^2, 0 = no agreement, 1 = full agreement). For plots see S 2.1 Fig. "Suitable" records for reporting rate and occupancy models are defined as records which meet certain quality criteria assumed to indicate that the recorder recorded against a complete species list – see section 2.3.2.2 above for a full definition.

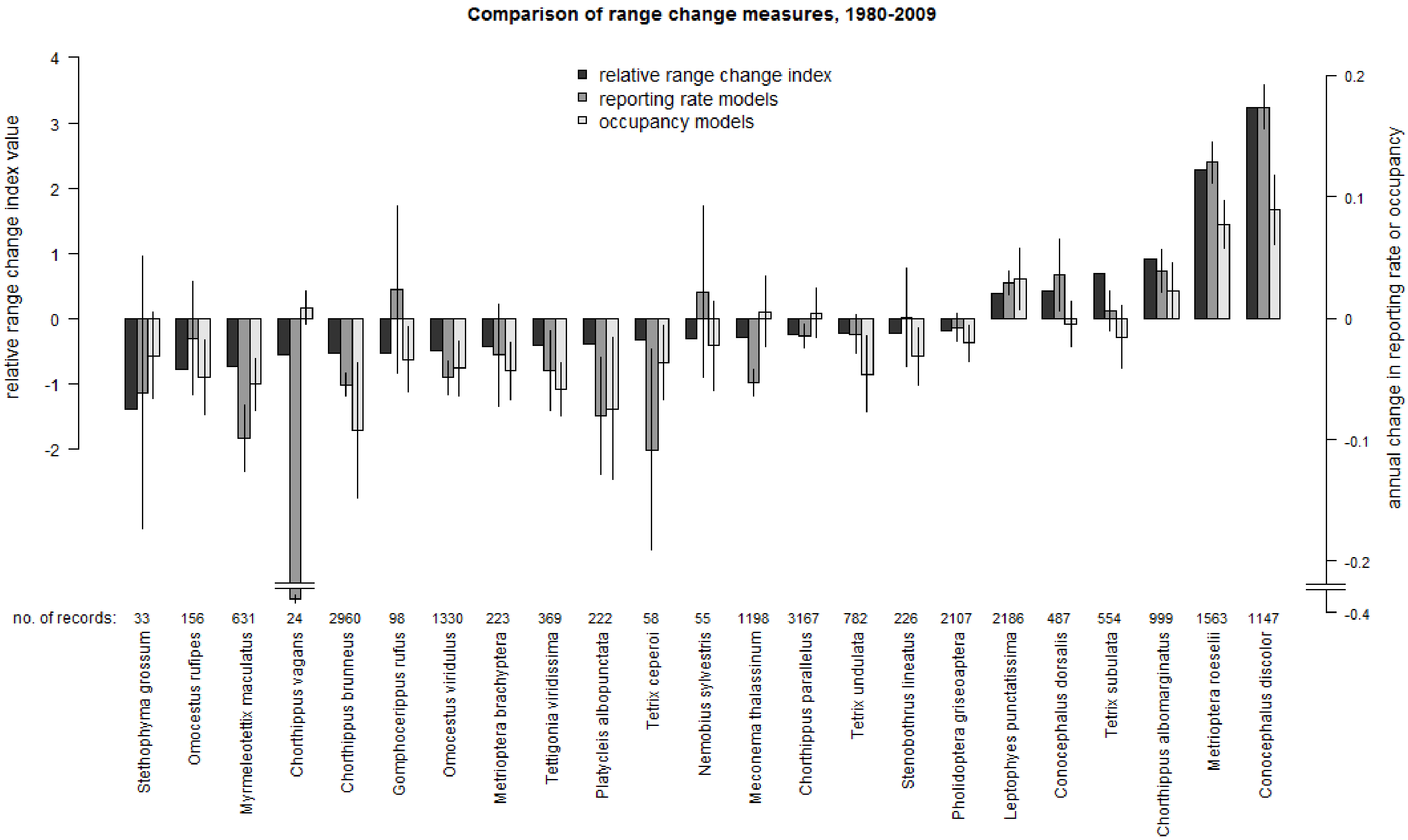


Fig. 2.20: Comparison of three distribution trend measures for Orthoptera in Britain, 1980-2009.
Comparison of relative range change index, reporting rate and occupancy models. Error bars indicate upper and lower 95% confidence intervals for the latter two measures. Numbers of records per species used in reporting rate and occupancy models are given above the species names. Species for which a relative range change index could not be calculated are excluded, i.e. species occurring in 5 or fewer surveyed hectads in the 1980-9 time period. Note y-axis is truncated between -0.2 and -0.4. See S 2.1 Table for detailed values.

It is apparent that while there is good agreement between distribution trend measures for species with good data quality and quantity, measures may diverge more for rare species and those with few "high quality" records, i.e. few records at the spatial and temporal resolution of individual site visits, and which are likely to be part of a species list (section 2.3.2.2). The trend estimates of the relative range change index for these rare species may be more reliable than those of the other two methods for this dataset, because the index is able to use all available records, including early records at low spatial and temporal resolutions. For example, the distribution of the Large Marsh Grasshopper *Stethophyma grossum* is known to have suffered a large decline between the 1980s and 2000s, losing all its populations outside Hampshire and Dorset (Benton 2012). This is reflected in its decadal hectad distribution (14 hectads in the 1980s, 7 hectads in the 2000s, S 2.1 Table) and large negative range change index. However, many of the early records (including from populations which went extinct) were unsuitable for use in the reporting rate and occupancy models due to their data quality requirements (high resolutions, minimum list length, minimum number of visits to a site): only records from 8 hectads were suitable, including the 7 hectads still occupied in the 2000s, and neither method produced a significant estimate of decline.

Altogether, therefore, the relative range change index is likely to be the distribution trend measure suitable for the largest number of species, but produces conservative estimates of change (Isaac et al. 2014). For species with sufficient quality and quantity of data (which is likely to exclude rare species), occupancy models are a statistically more powerful measure of change and they are more robust to biases than reporting rate models, albeit taking longer to compute. Finally, none of the methods discussed here are currently suitable for assessing the very rarest species (occupying 5 hectads or fewer). Table 2.6 summarises the comparison of the three distribution trend measures as applied here – their definition, calculation and outputs, assumptions made, how biases are addressed, advantages, disadvantages and recommendations for their use.

Table 2.6: Comparison of distribution trend analysis methods

		Relative range change index	Reporting rate model with effects of list length and site	Occupancy detection model with effects of list length and site
Definition and calculation of distribution trend		Change in proportion of surveyed squares occupied relative to mean change for species group. Calculated as standardised residuals of a linear model. A weighting by range size can be applied to account for greater variance among species with very small ranges.	Change in proportion of visits during which species is reported, allowing for variation by site and number of species recorded during visits. Modelled as change in reporting probability, using generalised linear mixed models (GLMMs) with a random effect of site and a fixed effect of list length.	Mean annual occupancy of sites (and derived from this, mean change in occupancy over the study period). Modelled as probability of occupancy while accounting for probability of detection, using hierarchically coupled Bayesian logistic models, with a random effect of site and a fixed effect of list length.
Output		Single relative range change index value per species without units or measure of error.	Single absolute value for each species of mean annual change over the study period in the probability of being detected, with standard error (on logit scale).	Annual absolute values of occupancy per species for each year of the study period, with credible intervals. Derived from this e.g. mean values of annual change in occupancy over study period (on logit scale).
Assumptions		Recorders aim to record as many species of the taxonomic group per grid square as they can during each time period. There are no changes in the recording of particular species between time periods.	Recorders record all species of the taxonomic group which they detect on each visit to a site. No changes in detectability over time. If list-lengths are included as a covariate they are assumed to reflect recording effort.	Recorders record all species of the taxonomic group which they detect on each visit to a site. Occupancy of sites does not change during “closure” periods (here years), i.e. no colonisation or extinction within years, only between years.
How are biases addressed?	**Uneven spatial sampling**	Only squares surveyed in both time periods are included in analysis.	A random effect for site is included.	A random effect for site is included in the state (presence-absence) model.
	Uneven temporal sampling	Linear model fitted to represent overall change in recording effort for the taxonomic group; individual species’ range changes calculated relative to this	Trend calculated as change in probability of reporting *per visit*.	Trend calculated as change in probability of occupancy, after controlling for probability of detection *per visit.*
	Uneven effort per visit	Data summarised at large temporal and spatial scales (over many visits).	If a covariate for list length is included this is assumed to reflect recording effort.	A fixed effect for list length is included in the observation (detection-nondetection) model.
	Uneven spatial and temporal precision	Records summarised at large spatial and temporal scales (usually 10km squares, and many years per time period)	Records should be summarised at one spatial and temporal scale across the study period which corresponds to typical visits, e.g. 1km squares and date specified to a day, and limited to records of at least these precisions.	Same as reporting rate models.
	Uneven detect-ability	Not explicitly addressed, but records are summarised at large spatial and temporal scales, averaging out changes in detectability accordingly.	Not explicitly addressed.	Detectability modelled in separate sub-model from repeat visits to sites each year.
Advantages		Robust to most biases. Can use all records including those at low temporal and spatial resolutions. Computationally un-intensive.	Robust to several biases. Good statistical power to detect change, because information from individual visits is used. Produces absolute value of change in reporting rate per species. Fairly easy to compute. Outputs easy to understand and communicate.	Robust to biases. Good statistical power to detect change, because information from individual visits is used. Produces annual, absolute values of occupancy per species. Outputs easy to understand and communicate.
Disadvantages		Low statistical power to detect trends. Range change values are purely *relative* to the average for the species group, an overall decline or increase for all species cannot be detected.	Requires high quality and quantity of data. Not robust to changes in detectability. Species with few records subject to producing misleading conclusions.	Requires high quality and quantity of data with repeat samples during “closure” periods (typically years). Computationally intensive.
Recommen-dations		Best used at large spatial and temporal scales over which complete coverage was attempted, e.g. comparison of national atlases. Suitable for conservative, relative assessment of whole species group, including rare species and low resolution records, excluding very rarest	Filter data to complete lists: e.g. threshold list lengths; sites with minimum numbers of visits; species with similar habitats and phenologies that are likely to be recorded together Summarise data at resolutions of typical visit, e.g. 1km^2 and 1 day. Exclude species with few records.	Same as reporting rate models. Best method for species with high quantity and quality of data.

2.5 Conclusion

Over five decades of operation since 1968, the Orthoptera Recording Scheme of Britain and Ireland has built up a database of records and mapped the distributions of Orthoptera and related species, and changes in these distributions. While recording has aimed to achieve national coverage at 10x10km resolution for several national atlases, and at finer resolutions where county atlases have been collated, recording is generally unstructured, with no standard protocol or measure of recording effort. This, and the development of the methods of recording and record sharing over time have resulted in a range of biases in the data, which need to be taken into account during data analysis. A number of statistical methods for distribution trend analysis have been developed to this end. Care is needed with setup of analyses in order to meet the assumptions made. Occupancy detection models provide a powerful and robust measure of distribution change for species with good quantities and quality of data. The “relative range change index” is the method suitable for the largest number of species, including those with low quantity and quality of data, although it has relatively low statistical power to detect change.

Orthoptera recorders today benefit from a range of accessible identification guides and convenient methods of record collection and submission, including a scheme website and a dedicated mobile app. A central online database makes record verification and provision of feedback more efficient for recording scheme organisers at national and county levels. The recording scheme should therefore be in a good position to maintain and build on its activities into the future. Some future perspectives for Orthoptera distribution recording are discussed in 6, and the scope for structured abundance monitoring is explored in chapter 5.

3. Two species with an unusual combination of traits dominate responses of British grasshoppers and crickets to environmental change

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3.1 Abstract

There are large variations in the responses of species to the environmental changes of recent decades, heightening interest in whether their traits may explain inter-specific differences in range expansions and contractions. Using a long-term distributional dataset, we calculated range changes of grasshoppers and crickets in Britain between the 1980s and the 2000s and assessed whether their traits (resource use, life history, dispersal ability, geographic location) explain relative performance of different species. Our analysis showed large changes in the distributions of some species, and we found a positive relationship between three traits and range change: ranges tended to increase for habitat generalists, species that oviposit in the vegetation above ground, and for those with a southerly distribution. These findings accord well with the nature of environmental changes over this period (climatic warming; reductions in the diversity and increases in the height of vegetation). However, the trait effects applied mainly to just two species, *Conocephalus discolor* and *Metrioptera roeselii*, which had shown the greatest range increases. Once they were omitted from the analysis, trait effects were no longer statistically significant. Previous studies on these two species emphasised wing-length dimorphism as the key to their success, resulting in a high phenotypic plasticity of dispersal and evolutionary-ecological feedback at their expanding range margins. This, combined with our results, suggests that an unusual combination of traits have enabled these two species to undertake extremely rapid responses to recent environmental changes. The fact that our results are dominated by two species only became apparent through cautious testing of the results' robustness, not through standard statistical checks. We conclude that trait-based analyses may contribute to the assessment of species responses to environmental change and provide insights into underlying mechanisms, but results need to be interpreted with caution and may have limited predictive power.

3.2 Introduction

The responses of individual species to environmental change are highly variable, despite average polewards and upwards range shifts of species responding to climate change, and contractions of species ranges in regions experiencing habitat loss, degradation and fragmentation (Thomas et al. 2004b, Hickling et al. 2006, Chen et al. 2011, Mair et al. 2012, IPCC 2014). Often, different environmental changes interact to affect species and result in a wide range of responses (Warren et al. 2001, Fox et al. 2014). At present, we have limited ability to predict the attributes of species that will thrive and exploit new opportunities, and of those that will decline and fail to adapt to changing conditions (Angert et al. 2011, Buckley and Kingsolver 2012). Understanding this variation represents a fundamental scientific challenge, the answers to which will have relevance to the conservation of species and species communities, and to the wider management of ecosystems.

The natural environment has been subject to extensive changes over recent decades. Global average surface air temperatures have risen by about 0.8°C since 1900, much of this rise occurring in the past 30 to 40 years, making the speed of recent warming faster than most past climatic changes (Wolff et al. 2014). The mean Central England Temperature in the 2000s was 0.84°C higher than in the 1980s (Parker et al. 1992). Globally, conversion of natural habitats to agriculture reached an unprecedented rate in the second half of the 20th century and this continues in most parts of the world. In contrast, in many developed countries conversion to agricultural use has slowed or stabilized (Millennium Ecosystem Assessment 2005a). In England, large areas of land were taken out of production as “set aside” from 1990 onwards, as a result of farming subsidies, and soon exceeded 10% of arable land, remaining at around this level until payments were stopped from 2008 (Defra 2010). However, agricultural practices continue to intensify at a global scale; nitrogen fixation through human activity, mainly fertilizer production, now equals or exceeds fixation in natural ecosystems, and considerable proportions are lost to the environment (Millennium Ecosystem Assessment 2005b). Large areas of the UK exceed “critical loads” of nutrient nitrogen, i.e. levels harmful to sensitive elements of the environment (Stevens et al. 2011). Such climatic and land use changes may strongly affect species communities and the matrix of habitats available; for example in Britain average plant species richness has decreased across habitats since 1978, with light-loving species of shorter turf declining and competitive species of fertile ground increasing (Carey et al. 2008).

We used grasshoppers and crickets (Orthoptera) as a model group to study the impacts of these changes and to identify traits which explain why species may vary in the extent to which their geographic ranges are changing. Grasshoppers and crickets are a suitable group because they are ectothermic insects found predominantly in open habitats, and are consequently highly responsive to climatic and land use changes (Willott and Hassall 1998, Simmons and Thomas 2004, Gardiner 2009, Cherrill 2010). In addition, the species in Britain display a broad range of biological traits (Benton 2012), which might underpin their different distribution changes (Angert et al. 2011). Many grasshoppers and crickets are easily observed and identified, and the "Orthoptera Recording Scheme" has produced a large dataset which is available for research (Orthoptera and Allied Insects Recording Scheme of Britain and Ireland 2014). Trait-based analyses have previously been carried out on temperate grasshoppers and relatives, including investigations of range sizes (Willott and Hassall 1998), extinctions (Reinhardt et al. 2005), degree of nestedness (Schouten et al. 2007), species richness (Marini et al. 2010, Hendriks et al. 2013) and community composition (Dziock et al. 2011), but none across species at a national scale with a focus on investigating range change.

We considered here a series of traits that might be expected to influence the responses of species to a variety of land use and climatic changes:

3.2.1 Resource use traits

Under conditions of environmental change, generalists that are capable of exploiting a wide range of resources are more likely to be able to survive changes to the availability of a specific resource in a landscape, and they are more likely than specialists to be able to exploit new landscapes if climatic or other conditions become suitable (Öckinger et al. 2010, Gallagher et al. 2015). Numbers of habitats exploited and diet are commonly used as measures for the degree of species' resource specialisation (Comont et al. 2012, Dapporto and Dennis 2013). Preferred vegetation structures and oviposition sites are two further traits that may describe species' resource requirements, because they play a critical role in determining the suitability of habitats in terms of microclimatic conditions, particularly for ectothermic insects (Sutherland and Hill 1995, Thomas et al. 2009, Suggitt et al. 2011, Bennie et al. 2013, Hendriks et al. 2013). We hypothesised that range changes would be positively related to traits indicative of microclimatic requirements favoured by recent land use change, i.e. a preference for medium or tall vegetation, and oviposition above ground.

3.2.2 Life history traits

Species' life history traits influence their rates of reproduction, and hence exert an important influence on their ability to respond to environmental change; for example the number of generations per year and body size (Whitman 2008, Angert et al. 2011). We predicted that the greatest range increases would be positively related to traits associated with fast reproduction, i.e. short generations, and small body size. Winter stage (i.e. life stage at which the species overwinters) and phenology (i.e. seasonal timing of the life cycle) may influence species' vulnerability to adverse weather and their ability to exploit favourable seasonal conditions (Roy and Sparks 2000, Altermatt 2010, Thackeray et al. 2010). For a group of species with the same over-winter stage, those that mature later in the season are likely to have a greater degree of "thermal limitation", i.e. to require a greater sum of warmth for development. We therefore predicted late-maturing species to have increased their ranges more, since they would be likely to benefit more from recent climatic warming.

3.2.3 Traits characterising dispersal ability

A critical factor determining species' capacity to respond to environmental change is their dispersal ability, particularly if the rate of that change is rapid (Simmons and Thomas 2004, Marini et al. 2010, Öckinger et al. 2010), although if habitat is highly fragmented selection may also act against dispersal (Travis and Dytham 2002). Wing length and wing load are species traits commonly used to approximate dispersal ability in insects (Hill et al. 1999). We predicted that increases in range would be positively related to wing morphology favouring dispersal – i.e. long wings or wing-length dimorphism, and low wing load. British grasshoppers and crickets include several species which exhibit wing dimorphism, with a short-winged (brachypterous) form and a long-winged, particularly dispersive (macropterous), form. Strong trade-offs between investment in the flight apparatus and investment in reproductive organs mean that wing-dimorphic species may be at a selective advantage by producing increased numbers of macropterous individuals only under conditions favouring dispersal (Simmons and Thomas 2004, Dziock et al. 2011). Therefore, wing-dimorphic species were predicted to have shown more positive distribution trends over the recent decades of environmental change than obligate macropters or obligate brachypters.

3.2.4 Distributional traits

Parameters of species’ distributions including average latitude or position of distributional margins have been used as measures of their climatic requirements (Hickling et al. 2006). Species with lower average latitudes are likely to be more thermally limited than those with higher ones and hence to benefit more from warming; we therefore predicted a negative relationship between average latitude and range change.

Using these biological traits and hypotheses, we assessed their relative importance in explaining distributional changes of grasshoppers and crickets in Britain between the 1980s and 2000s.

3.3 Materials and Methods

3.3.1 Range changes

The extent of changes in distributions of British grasshoppers and crickets was quantified using the data of the Orthoptera Recording Scheme (Orthoptera Recording Scheme 2013a, b, Orthoptera and Allied Insects Recording Scheme of Britain and Ireland 2014). The scheme has collated 104,144 distribution records from over 2,000 volunteers since 1967. Records are mostly gathered in a non-standardised way, i.e. with no standard protocol or measure of recording effort, the main aim being to record distributions. Locations are recorded to varying degrees of precision, many to a 100m grid square resolution or finer (55%), with the rest at 1km, 2km or 10km resolutions (27%, 3% and 15% respectively). Data were summarised at a 10km grid square (“hectad”) resolution, based on the British National Grid, and the analysis was restricted to the mainland and inshore islands of Great Britain (England, Scotland, Wales). All calculations were performed in the statistical software environment “R”, version 3.0.2 (R Core Team 2013).

Changes in species range sizes were calculated between the decades 1980-89 and 2000-09. These periods were selected to cover the time of most intense recording and therefore to maximise the number of records available for analysis while maintaining a gap between them. The periods were also selected to cover a time of extensive environmental change both in climate and land use (mean Central England Temperature increasing by 0.84°C; in excess of 10% of arable land taken out of cultivation; and nutrient enrichment of many habitats continuing – resulting in vegetation becoming taller, more shaded and less diverse (Parker et al. 1992, Carey et al. 2008, Defra 2010, Stevens et al. 2011); cf. Introduction and Discussion).

Range changes were calculated from grid cells that had been surveyed in both time periods in order to minimise any effect of differences in the number of grid cells visited or the geographical pattern of recording. To understand impacts of increasing recorder effort on range change measures, four sets of these “surveyed squares” were defined: hectads with a minimum, respectively, of one, two, three or four grasshopper or cricket species recorded in both time periods (these were not necessarily the same species in both periods) (Fig. 3.1, cf. (Hickling et al. 2006)). Range change measures were calculated for each of these four sets of “surveyed squares” / levels of recording effort, and Pearson’s correlation tests carried out between them in order to assess their consistency. For all levels of recording effort, the majority of "surveyed squares" were located in the southern half of England with lower numbers in northern England, Wales and Scotland; this is not surprising as it reflects grasshopper and related species diversity as well as human population (and hence recorder) density, but it should be borne in mind when interpreting results.

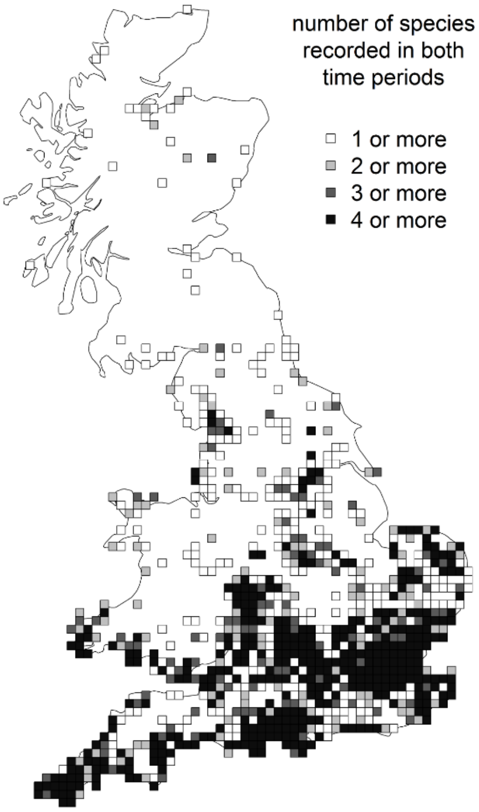


Fig. 3.1. Location of four sets of "surveyed squares" with different levels of recording effort.

10km grid squares on the British mainland and inner islands with respectively at least one, two, three or four grasshopper or related species recorded in both the periods 1980-9 and 2000-9. There was a total of 844 squares with at least one species recorded in both time periods (32% of the possible total of 2,662 squares), 598 squares (22%) with at least two species, 474 squares (18%) with at least three, and 375 squares (14%) with at least four.

Species range changes were calculated in two ways: (1) "Uncorrected range change" was defined simply as the absolute difference between the (logit-transformed) proportion of "surveyed squares" occupied by each species in the 2000s vs. the 1980s. Proportions were logit-transformed in order to create unbounded distributions and help to achieve normality (Williamson and Gaston 1999). (2) “Corrected range change”: The dataset showed an approximate doubling of recording effort between the 1980s (13,188 records for the species investigated here) and the 2000s (26,239 records). We therefore calculated a relative range change index which measured the difference in the observed range change of each species relative to the mean observed change for the whole taxonomic group, thus accounting for overall changes in recording effort (albeit at the cost of providing a purely relative measure) (Telfer et al. 2002). The index was calculated by fitting a linear regression of the logit-transformed proportions of “surveyed squares” occupied by species in the 2000s vs. the 1980s; the standardised residuals of this regression were defined as the relative index. This “corrected range change” (“Telfer”) has been shown to be robust to multiple potential biases in recording, if rather conservative (Isaac et al. 2014). In order to further check that observed range changes were genuine and not influenced unduly by large one-off population fluctuations we plotted annual relative numbers of hectads recorded per species over the entire study period 1980-2009 for species with large range change values.

Grasshopper, cricket and bush-cricket species native to Britain were included in the analyses; species occupying fewer than five hectads in the 1980s were excluded, because for the rarest species small changes in distribution or recording may affect trend calculations disproportionately (Telfer et al. 2002). This left a total of 23 species for the present study (Table 3.1).

3.3.2 Species traits

A database of British grasshopper and related species traits covering habitat and resource use, life history, dispersal ability, and distribution was compiled to address the hypotheses of factors affecting range change outlined in the introduction (Tables 3.1 and 3.2).

Table 3.1. Species traits, range sizes, and “uncorrected range change” and “corrected range change” values.

species		habitat and resource use				life history				dispersal ability		distri-bution	raw grid square counts, percentage changes & range change measures (based on “surveyed squares” with at least 1 species recorded)					
Scientific name	English name	(i) breadth of habitat use	(ii) preferred vegetation structure (short S, medium M, tall T)	(iii) oviposition site (ground G, ground or vegetation GV, vegetation V)	(iv) diet (herbivorous H, not herbivorous not_H)	(v) mean body size (mm)	(vi) number of generations per year (one O, half H, half or one HO)	(vii) winter stage (egg E, larva or adult not_E)	(viii) phenology: month quarter of first appearance of adults	(ix) wing morph (short S, long L, dimorphic D)	(x) wing load	(xi) average latitude	range size 1980-9 (no. of "surveyed squares" occupied)	range size 2000-9 (no. of "surveyed squares" occupied)	% change in range size	"uncorrected range change"	"corrected range change" , all species	"corrected range change" , excluding *C. discolor* and *M. roeselii*
Meconema thalassinum	Oak bush-cricket	4	T	V	not_H	15.0	HO	E	7.75	L	0.043	51.70	315	294	-7	-0.11	-0.34	-0.41
Tettigonia viridissima	Great green bush-cricket	3	M	G	not_H	32.5	H	E	7.5	L	0.043	51.01	139	125	-10	-0.13	-0.43	-0.39
Pholidoptera griseoaptera	Dark bush-cricket	5	T	V	not_H	17.5	HO	E	7.5	S	0.001	51.45	405	401	-1	-0.02	-0.19	-0.18
Platycleis albopunctata	Grey bush-cricket	2	M	GV	not_H	20.0	O	E	7.25	L	0.038	50.67	52	49	-6	-0.06	-0.43	-0.16
Metrioptera brachyptera	Bog bush-cricket	1	M	V	not_H	15.0	H	E	7.5	D	0.107	51.69	74	68	-8	-0.09	-0.44	-0.26
Metrioptera roeselii	Roesel’s bush-cricket	6	M	V	not_H	16.5	HO	E	6.75	D	0.118	51.65	71	332	+368	1.95	2.31	
Conocephalus discolor	Long-winged conehead	10	M	V	not_H	19.0	O	E	7.75	D	0.042	50.82	46	378	+722	2.63	3.23	
Conocephalus dorsalis	Short-winged conehead	6	M	V	not_H	14.5	O	E	7.75	D	0.089	51.50	137	213	+55	0.55	0.48	1.53
Leptophyes punctatissima	Speckled bush-cricket	4	T	V	H	13.5	HO	E	7.75	S	0.001	51.41	337	424	+26	0.42	0.39	1.10
Nemobius sylvestris	Wood cricket	2	T	G	not_H	8.5	H	not_E	6.0	S	0.015	50.82	18	19	+6	0.05	-0.36	0.24
Tetrix ceperoi	Cepero’s groundhopper	5	S	GV	H	9.0	O	not_E	5.0	L	0.130	50.84	25	27	+8	0.08	-0.30	0.29
Tetrix subulata	Slender groundhopper	7	S	GV	H	10.0	O	not_E	4.25	D	0.127	51.54	171	282	+65	0.68	0.67	1.87
Tetrix undulata	Common groundhopper	9	S	GV	H	9.0	O	not_E	3.75	D	0.137	51.78	309	298	-4	-0.06	-0.27	-0.26
Stethophyma grossum	Large marsh grasshopper	2	M	GV	H	27.0	O	E	7.75	L	0.022	50.89	14	7	-50	-0.67	-1.40	-1.90
Stenobothrus lineatus	Stripe-winged grasshopper	4	S	GV	H	20.5	O	E	6.25	L	0.020	51.30	68	72	+6	0.06	-0.24	0.18
Omocestus rufipes	Woodland grasshopper	1	M	G	H	16.5	O	E	6.0	L	0.035	50.97	49	37	-24	-0.29	-0.74	-0.81
Omocestus viridulus	Common green grasshopper	8	M	GV	H	18.5	O	E	5.75	L	0.027	52.25	402	350	-13	-0.25	-0.51	-0.85
Chorthippus brunneus	Field grasshopper	7	S	G	H	19.0	O	E	5.75	L	0.033	51.90	553	500	-10	-0.27	-0.50	-0.98
Chorthippus vagans	Heath grasshopper	3	M	G	H	17.0	O	E	7.25	L	0.027	50.75	6	6	0	0.00	-0.54	0.14
Chorthippus parallelus	Meadow grasshopper	14	M	G	H	18.0	O	E	6.0	D	0.034	51.73	526	503	-4	-0.11	-0.29	-0.50
Chorthippus albomarginatus	Lesser marsh grasshopper	6	M	GV	H	18.0	O	E	7.0	L	0.025	51.70	123	241	+96	0.85	0.87	2.37
Gomphocerippus rufus	Rufous grasshopper	5	M	G	H	19.0	O	E	7.75	L	0.023	51.23	27	25	-7	-0.08	-0.51	-0.17
Myrmeleotettix maculatus	Mottled grasshopper	7	S	G	H	14.0	O	E	5.75	L	0.040	52.15	206	157	-24	-0.34	-0.70	-1.04

For definitions of traits see Table 3.2, for details of calculation of range change measures see text.

Table 3.2. Definitions of species traits and sources of information.

	trait		definition	source
habitat and resource use	(i)	*breadth of habitat use*	total number of habitat types known per species (mean ± s.d. = 5.3 ± 3.1); log-transformed	summary table of habitats in (Evans and Edmondson 2007)
	(ii)	*preferred vegetation structure*	typical vegetation height of species' habitats: "Short": open ground, short vegetation <=20cm (6 species). "Medium": medium or long herbaceous vegetation >20cm, patchy, early succession scrub (13 species). "Tall": woodland, trees, hedgerows and medium or late succession scrub (4 species).	"habitat" sections of species accounts in (Benton 2012); the categories in the present study summarise those in (Oschmann 1991): "Tall" = V1-V5, "Medium" = V6-V8, "Short" = V9.
	(iii)	*oviposition site*	"Ground": eggs laid exclusively in the ground (8 species). "Vegetation": eggs laid exclusively in vegetation (7 species). "Ground or vegetation": eggs laid in ground or vegetation (8 species). The latter are species which oviposit at the soil surface or at the base of plants.	"life cycle" sections of species accounts in (Benton 2012)
	(iv)	*diet*	preferred food of each species: "herbivorous" (14 species) "not herbivorous" i.e. omnivorous or carnivorous (9 species)	species accounts in (Benton 2012) and (Marshall and Haes 1988)
life history	(v)	*mean body size*	mean of minimum and maximum body lengths excluding wings (mean ± s.d. = 16.9 ± 5.9mm); log-transformed	species accounts in (Detzel 1998)
	(vi)	*number of generations per year*	"One": species requires one year to mature (16 species). "Half": species always requires at least two years to mature (3 species). "Half or One": species may develop in one or more years (4 species)	"life cycle" sections of species accounts in (Benton 2012).
	(vii)	*winter stage*	developmental stage in which the species overwinters: "Egg" (19 species). "Not egg" (i.e. nymph or adult) (4 species)	"life cycle" sections of species accounts in (Benton 2012)
	(viii)	*phenology*	time of year when adults first appear, to the nearest quarter of a month (mean across species = 6.6, i.e. in the third quarter of June; s.d. = 1.2, i.e. just over one month)	"life cycle" sections of species accounts in (Benton 2012)
dispersal ability	(ix)	*wing morph*	"Short": wings never reach to end of abdomen and species is always flightless (3 species). "Long": wings may reach to end of abdomen or beyond (and species does not display wing-length dimorphism) (13 species). "Dimorphic": species exhibits wing-length dimorphism (7 species)	species accounts in (Benton 2012)
	(x)	*wing load*	ratio of the square of a species' mean wing length (in mm) to the cube of a species' mean body length (in mm) as calculated in (v) above. Square of wing length was used as proxy for wing area, and cube of body length as proxy for body mass (Dudley 2002), since actual measurements were not available in the literature for all species (mean ± s.d. = 0.051 ± 0.043)	species accounts in (Marshall and Haes 1988). No wing length measurements were available for *Tetrix* species; for these, pronotum lengths in (Detzel 1998) were used instead, which approximate hind wing length (Benton 2012). For wing-dimorphic species, wing lengths of macropters were used.
distribution	(xi)	*average latitude*	average latitude of hectads occupied by a species in 1980-9; only "surveyed squares" with at least one species recorded in both 1980-9 and 2000-9 were considered (mean ± s.d. = 51.38 ± 0.46 degrees north)	calculated from Orthoptera Recording Scheme distribution dataset (Orthoptera Recording Scheme 2013a, b)

To avoid potential problems with collinearity between explanatory variables, correlations between traits were investigated using a method employed by (Pocock et al. 2006): Pearson's correlation tests were calculated between continuous variables, Kendall's correlation tests between categorical variables, and Kruskal-Wallis tests between continuous and categorical variables. A sequential Bonferroni correction was applied in order to account for the large number of tests conducted (55) (Holm 1979). No significant correlations were found.

To investigate the relationships between distribution changes and species traits we fitted Generalised Linear Models (GLMs) with Gaussian errors, using first "uncorrected range change" as dependent variable and then repeating analyses with "corrected range change" values. In order to understand the relative importance of different traits in driving distribution changes we took a multi-model inference approach, fitting all possible combinations of trait variables, selecting a set of top models by Akaike information criterion (AIC), and averaging the coefficients and standard errors of trait variables across these (Akaike 1974, Burnham and Anderson 2002): We fitted GLMs for all 2,047 combinations of the 11 explanatory trait variables and calculated AIC values and differences to the best model with the lowest AIC (ΔAIC). Models with ΔAIC < 4 were selected as the top set for which there was considerable statistical support (Burnham and Anderson 2002). The percentages of top models in which each trait occurred were then calculated. In order to measure the relative importance of each trait, AIC values were transformed to "Akaike weights" (Burnham and Anderson 2002, Wagenmakers and Farrell 2004), and using these weights, means of trait coefficients across top models were calculated with the "weighted.mean" function in R. Weighted mean standard errors of coefficients were calculated using the following formula adapted from (Burnham and Anderson 2002):

$$SE(b_{all}) = \sum_{i=1}^{n} w_i \sqrt{[SE(b_i)]^2 + [b_i - b_{all}]^2}$$

where *n* is the number of models, w_i is the Akaike weight of model *i*, $SE(b_i)$ is the standard error of coefficient *b* in model *i*, and b_{all} is the weighted mean of all coefficients *b*. Akaike weights were scaled so that their sum equalled 1 for each predictive variable, i.e. w_i values were divided by the sum of Akaike weights of all models which included the variable whose mean standard error was to be calculated. Confidence intervals (CI) across top models were then calculated by multiplying the weighted mean standard errors with factors of 1.96 (95% CI), 2.58 (99% CI) and 3.29 (99.9% CI) and adding / subtracting them from the weighted means of coefficients. Significance levels were assigned accordingly where the values did not span zero (* for 95% CI, ** for 99% CI, *** for 99.9% CI). Throughout this part of the analysis, range change values calculated from the largest set of "surveyed squares" (with a minimum of one species recorded in both time periods, i.e. with the minimum adequate level of recording effort) were used as our primary measures, and results were then compared to those obtained with the other three sets of "surveyed squares" i.e. higher levels of recording effort, in order to assess the robustness of our findings.

All analyses of relationships between distribution changes and species traits were also repeated with the exclusion of two species with particularly large range change values, *Conocephalus discolor* and *Metrioptera roeselii* (see below).

To assess the validity of using Gaussian GLMs with our data we plotted normal quantile-quantile plots of residuals of top sets of models and carried out Shapiro-Wilk tests for normality (Shapiro and Wilk 1965, Royston 1982).

To assess the overall goodness-of-fit of top models the amount of deviance accounted for by each model was calculated:

$$D^2 = [\text{null deviance} - \text{residual deviance}] / \text{null deviance}$$

This was adjusted to take into account the number of observations, i.e. species (s) and the number of predictors, i.e. traits (t) (Guisan and Zimmermann 2000, Weisberg 2013):

$$\text{adjusted } D^2 = 1-[(s-1)/(s-t)]*[1-D^2]$$

To give an overall fit of the top models, adjusted D^2 values were averaged, weighted by AIC weights as with the model coefficients before.

Fitted values of range change were extracted for the top models, and means weighted by model Akaike weights were calculated.

We investigated the potential influence of phylogenetic autocorrelation, i.e. non-independence of trait values due to relatedness between species, based on a method employed by (Comont et al. 2012). A "working phylogeny" (Grafen 1989) of the study species was drawn based on the taxonomy of the Orthoptera Species File (Eades et al. 2013) in the programme "Treemaker" (Crozier et al. 2005) with all branch segment lengths assumed to be equal (S 3.1 Fig.). A phylogeny may be approximated in this way based on taxonomic divisions where the true phylogeny is not (fully) known; assuming equal branch lengths and allowing more than two daughters per node reflects the lack of comprehensive detailed knowledge about the order of splitting (Grafen 1989). The “working phylogeny” was exported in “nexus” format and imported into R. The expected covariance between species was calculated using the “vcv” function in the R package “ape” and Moran’s I autocorrelation indices were calculated on the residuals of each of the top models using the “Moran.I” function. Moran’s I can take values from −1 (perfect negative autocorrelation) to +1 (perfect positive autocorrelation), with values around zero indicating independence of residuals between related species (Moran 1950, Paradis et al. 2004, Paradis 2011). Where Moran’s I indices were significant or near-significant, phylogenetically corrected models were fitted using the “pgls” function in the R package “caper” (Freckleton et al. 2002, Orme et al. 2013); as with GLMs before, models were initially fitted to all possible combinations of trait variables and results were then averaged across a set of top models with ΔAIC<4.

3.4 Results

3.4.1 Range changes

Our analysis of grasshopper and related insect range changes in Britain between the 1980s and 2000s showed moderate or large range size increases for a few species, with range size decreases for a smaller number, and less or no consistent change for the remaining majority of species. The species with the largest positive range changes were *Conocephalus discolor*, *Metrioptera roeselii*, *Chorthippus albomarginatus* and *Tetrix subulata*; those with the largest range size decreases were *Stethophyma grossum* and *Myrmeleotettix maculatus* (Fig. 3.2).

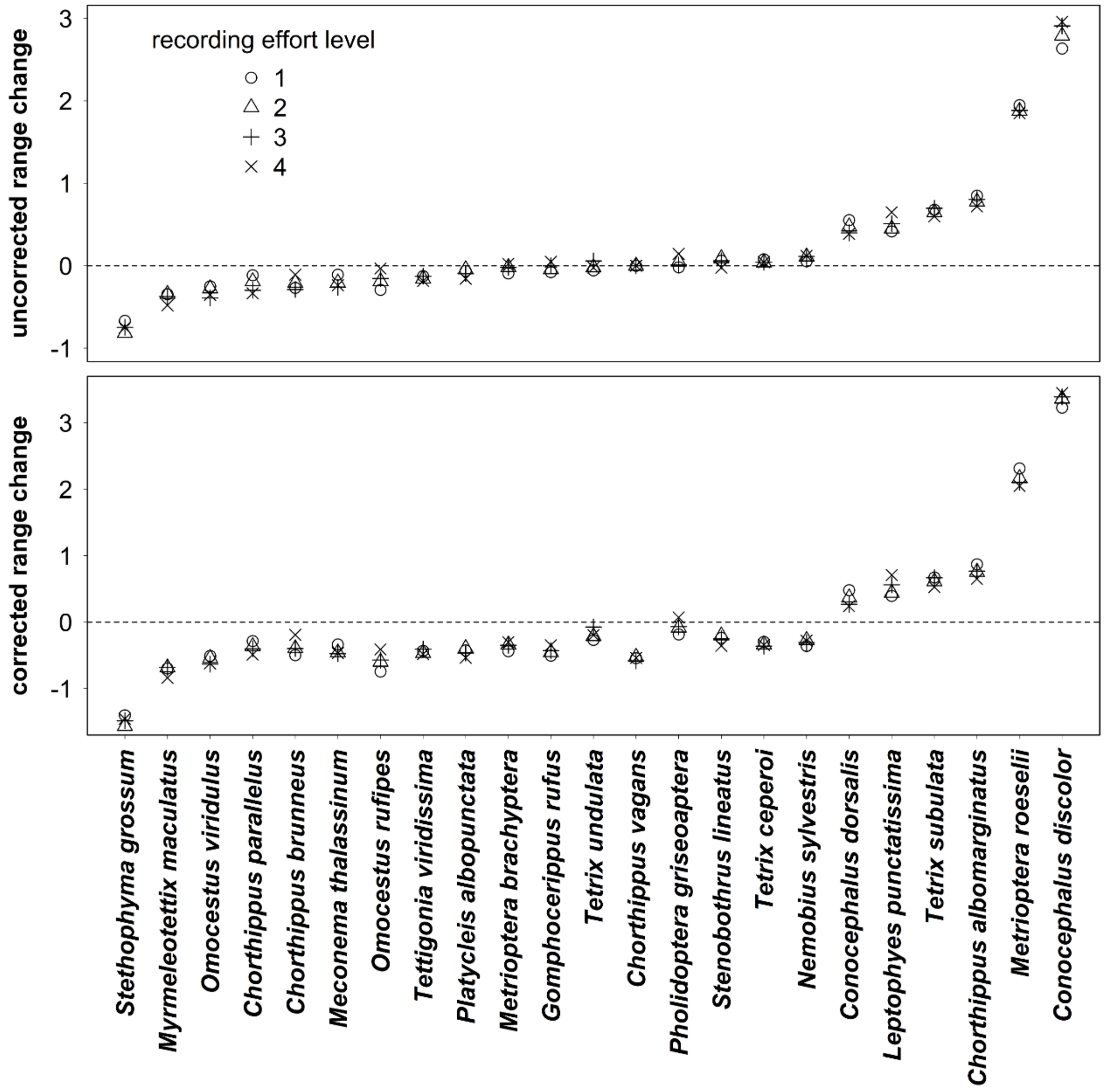


Fig. 3.2. Range changes of grasshoppers and related species in Britain between 1980-9 and 2000-9.

The figure shows “uncorrected” and “corrected range change” values for four levels of recording effort – i.e. based on four sets of “surveyed squares” with a minimum of 1 to 4 grasshopper or related species recorded in both time periods. Species are arranged in order of average uncorrected change. Note different y-axis scales.

There was a very high degree of consistency of range change values both across levels of recording effort and between “uncorrected” and “corrected” range change measures (Pearson’s r = 0.975 or greater, across all sets of range change values; Fig. 3.3, Table 3.3, S 3.1 Table).

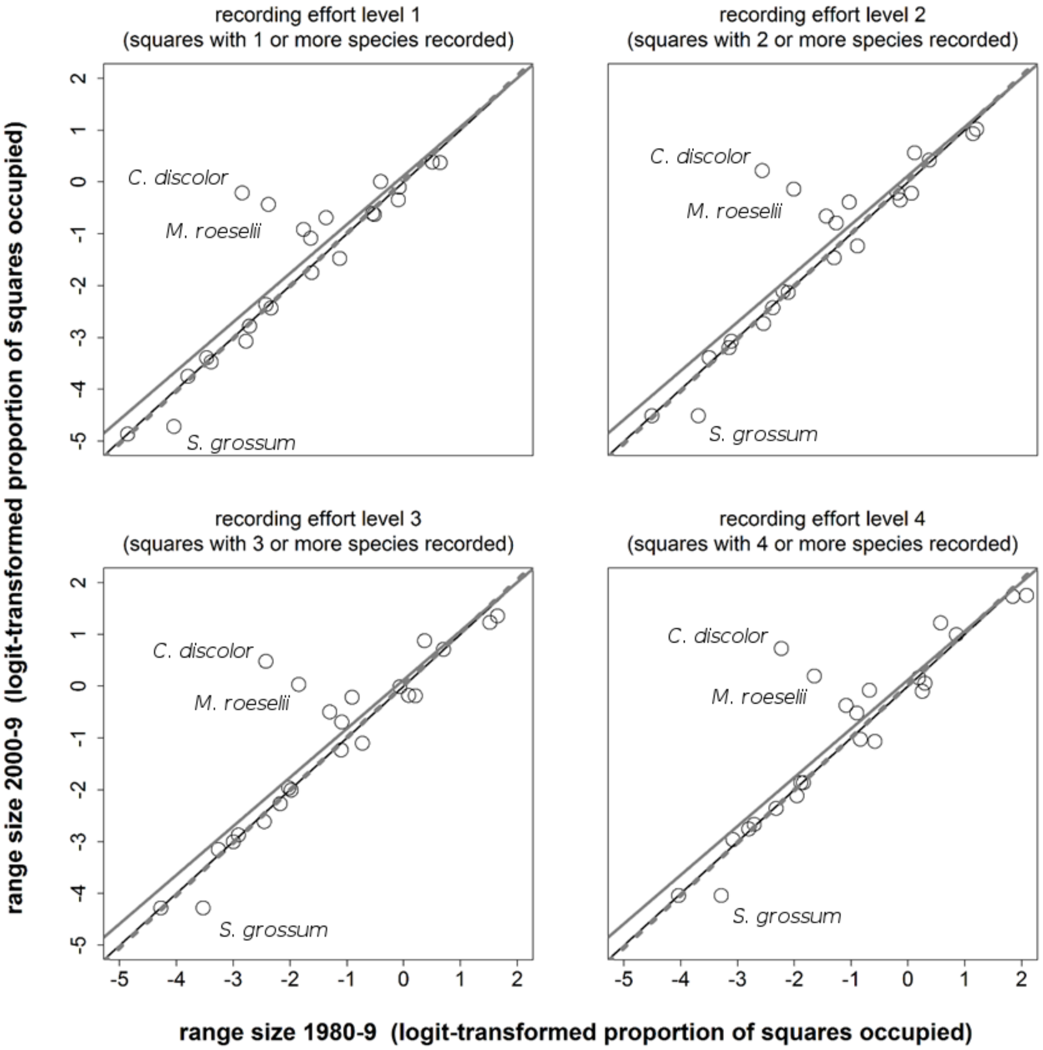


Fig. 3.3. Grasshopper and related species range sizes in 1980-9 and 2000-9 and calculation of range change measures.

The figure plots range sizes in 1980-9 vs. 2000-9 (as logit-transformed proportions of squares occupied) for four levels of recording effort. “Uncorrected range change” was defined as the absolute change in range size, i.e. residual distances from the (black) 1:1 unity lines. “Corrected range change” was defined as change in range size relative to the mean change across species, i.e. as the (standardised) residual distances from the linear regression lines (solid grey for all species, dashed grey for species excluding the two with particularly large range change values, *C. discolor* and *M. roeselii*).

Table 3.3. Correlation between range change values.

			"uncorrected range change"			"corrected range change"			
			level of recording effort (minimum number of species recorded in "surveyed squares")			level of recording effort (minimum number of species recorded in "surveyed squares")			
			2	3	4	1	2	3	4
"uncorrected range change"	level of recording effort (minimum number of species recorded in "surveyed squares")	1	0.996	0.992	0.983	0.994	0.989	0.985	0.975
		2		0.998	0.993	0.99	0.994	0.991	0.986
		3			0.995	0.983	0.988	0.989	0.984
		4				0.975	0.985	0.986	0.991
"corrected range change"	level of recording effort (minimum number of species recorded in "surveyed squares")	1					0.996	0.993	0.982
		2						0.998	0.992
		3							0.995

Pearson's correlation test values between "uncorrected" and "corrected range change" and four levels of recording effort.

Plots of annual relative numbers of hectads recorded per species showed trajectories consistent with our calculated range change values, and none of these annual series were indicative of a one-off population outbreak (S 3.2 and S 3.3 Figs.).

Two species, *Conocephalus discolor* and *Metrioptera roeselii* had undergone particularly large range changes compared to the other species (Fig. 3.2). In terms of the observed values of range change, they were statistical outliers (Grubbs' test for outliers: *C. discolor* (G = 3.25, p = 0.0018) and *M. roeselii* (G = 3.43, p = 0.0004) for "uncorrected range change", recording effort level 1). There were equivalent test results for all levels of recording effort and both range change measures (S 3.2 Table). As a matter of caution, therefore, the subsequent traits analysis was repeated with the exclusion of *C. discolor* and *M. roeselii*, and results compared to those for all species. As detailed below, however, on the basis of the residuals of the trait-based models these species were not statistical outliers so we present and discuss both sets of results.

3.4.2 Species traits, results for all species

The analysis of relationships between distribution changes and species traits for *all* species showed three traits to be significantly associated with changes in range for both range change measures (Table 3.4). Firstly, habitat breadth: species that used a greater number of habitats had increased their ranges to a significantly greater extent than those which occurred in fewer habitats (or vice versa) (slope $b=1.38$ for uncorrected range change, $b=1.95$ for corrected range change, $p<0.01$ for both). This trait was included in 100% of top models with ΔAIC<4 (top models comprised a set of 47 models for uncorrected, and 53 models for corrected range change). Secondly, oviposition site: for species that oviposited in vegetation, range size increased significantly more than for species that oviposited either in the ground or in the ground or vegetation (or vice versa) ($b=1.07$ / $b=0.98$ for uncorrected, and $b=1.47$ / $b=1.35$ for corrected range change, $p<0.01$ / $p<0.05$ for both). The oviposition site trait was also included in 100% of top models. The third significant association showed that for species occurring at greater average latitude (i.e. species whose distributions extended further northwards) range size decreased to a greater extent than for species with more southern average latitudes (or conversely, for species with more southern average latitudes range sizes had increased significantly more) ($b=-0.76$ for uncorrected, $b=-0.90$ for corrected range change, $p<0.05$ for both). This trait was included in 100% and 98% of top models for uncorrected and corrected range change respectively.

Table 3.4. Impacts of species traits on distribution changes of British grasshoppers and crickets (all species) between the 1980s and 2000s.

		“uncorrected range change”				“corrected range change”			
	trait	% included	weighted mean coefficient	weighted mean standard error	significance	% included	weighted mean coefficient	weighted mean standard error	significance
(Intercept)		100	39.09	16.36	*	100	45.17	22.48	*
habitat and resource use	(i) breadth of habitat use	100	1.38	0.48	**	100	1.95	0.64	**
	(ii) vegetation structure:	45				45			
	short vs. medium		-0.25	0.38	n.s.		-0.35	0.53	n.s
	short vs. tall		0.49	0.55	n.s.		0.56	0.73	n.s
	medium vs. tall		0.74	0.44	n.s.		0.91	0.57	n.s
	(iii) oviposition site:	100				100			
	vegetation vs. ground		1.07	0.38	**		1.47	0.51	**
	vegetation vs. ground or vegetation		0.98	0.42	*		1.35	0.58	*
	ground vs. ground or vegetation		-0.09	0.29	n.s.		-0.12	0.39	n.s
	(iv) diet:	21				26			
	herbivorous vs. not herbivorous		-0.08	0.35	n.s.		-0.18	0.47	n.s
life history	(v) mean body size	26	-0.50	1.29	n.s.	26	-0.26	1.78	n.s
	(vi) generations per year:	11				9			
	one vs. half		-0.32	0.48	n.s.		-0.45	0.64	n.s
	one vs. half or one		-0.21	0.67	n.s.		-0.25	0.88	n.s
	half vs. half or one		0.12	0.62	n.s.		0.20	0.82	n.s
	(vii) winter stage:	28				30			
	egg vs. not egg		0.01	0.63	n.s.		0.13	0.91	n.s
	(viii) phenology	30	-0.17	0.21	n.s.	38	-0.26	0.29	n.s
dispersal ability	(ix) wing morph:	21				19			
	short vs. long		0.12	0.78	n.s.		0.22	1.06	n.s
	short vs. dimorphic		-0.14	0.92	n.s.		-0.18	1.19	n.s
	long vs. dimorphic		-0.27	0.42	n.s.		-0.40	0.53	n.s
	(x) wing load	40	0.32	0.32	n.s.	38	0.39	0.46	n.s
distribution	(xi) average latitude	100	-0.76	0.32	*	98	-0.90	0.43	*

Summary of results for sets of top GLM models with ΔAIC<4 (47 models for “uncorrected range change”, and 53 models for “corrected range change”). The importance of traits is indicated by the frequency with which they are included in the top model set (% included), and by their weighted mean coefficients, standard errors and significance levels. Significance levels: *= p<0.05, **=p<0.01. Results given are for minimum adequate recording effort, i.e. for “surveyed squares” with a minimum of 1 species recorded in both 1980-9 and 2000-9. Results were highly consistent across all levels of recording effort and both range change measures, with the same three significant associations found in each case, and significant traits included in similar percentages of top models. Since there were no differences between results with different levels of recording effort, only those for minimum adequate levels of recording effort are presented.

Normal quantile-quantile plots and Shapiro-Wilk tests of residuals of the top sets of models revealed very little deviation from normality: tests had a median p-value of 0.410 for "uncorrected range change", and a median p-value of 0.418 for "corrected range change", with between 98% and 100% of top models showing no significant deviation from normality ($p>=0.05$) across all levels of recording effort and both range change measures (S 3.3 Table). We therefore concluded that using Gaussian GLMs with our data was valid in this respect.

Similarly, the analysis of phylogenetic autocorrelation in the top GLMs by calculation of Moran's I indices yielded low, non-significant index values for between 95% and 100% of top models for both range change measures and all levels of recording effort (S 3.4 Table). Subsequent fitting and selection of phylogenetically corrected "pgls" models did not change the results obtained with non-phylogenetic GLMs: The same numbers of top models were selected, with the same predictors and virtually identical coefficient and p-values as in GLMs (S 3.5 Table). Lambda values were consistently estimated as the default minimum permitted in the pgls function, $1\text{x}10^{-6}$. We therefore concluded that these results were indicative of a low phylogenetic signal and hence the analysis with non-phylogenetically-corrected GLMs was robust.

Calculation of adjusted D^2 values showed fairly high overall goodness-of-fit across top models with *all* species: the weighted means of adjusted D^2 values were 0.54 (minimum 0.03, maximum 0.59) and 0.56 (minimum 0.03, maximum 0.61) for "uncorrected" and "corrected range change" respectively. These were the values for the minimum adequate level of recording effort, and very similar ones were obtained for higher levels of recording effort (S 3.6 Table).

3.4.3 Species traits, results excluding *Conocephalus discolor* and *Metrioptera roeselii*

When the analysis of the relationships between distribution changes and species traits by GLMs was repeated for all species *excluding* the two species with particularly large range changes, *Conocephalus discolor* and *Metrioptera roeselii*, no traits were found to be significantly associated with changes in range for either measure of range change (Table 3.5).

Table 3.5. Impacts of species traits on distribution changes of British grasshoppers and crickets (excluding *Conocephalus discolor* and *Metrioptera roeselii*) between the 1980s and 2000s.

		"uncorrected range change"				"corrected range change"			
	trait	% included	weighted mean coefficient	weighted mean standard error	significance	% included	weighted mean coefficient	weighted mean standard error	significance
(Intercept)		100	0.98	3.12	n.s.	100	3.71	8.94	n.s.
habitat and resource use	(i) breadth of habitat use	49	0.38	0.30	n.s.	47	0.97	0.88	n.s.
	(ii) vegetation structure:	3				5			
	short vs. medium		-0.13	0.24	n.s.		-0.31	0.73	n.s.
	short vs. tall		-0.01	0.30	n.s.		0.16	0.93	n.s.
	medium vs. tall		0.12	0.25	n.s.		0.46	0.71	n.s.
	(iii) oviposition site:	24				22			
	vegetation vs. ground		0.24	0.24	n.s.		0.56	0.73	n.s.
	vegetation vs. ground or vegetation		0.04	0.26	n.s.		-0.01	0.79	n.s.
	ground vs. ground or vegetation		-0.20	0.18	n.s.		-0.57	0.51	n.s.
	(iv) diet:	20				18			
	herbivorous vs. not herbivorous		-0.03	0.19	n.s.		-0.06	0.53	n.s.
life history	(v) mean body size	59	-1.06	0.72	n.s.	67	-3.24	2.08	n.s.
	(vi) generations per year:	2				4			
	one vs. half		0.02	0.24	n.s.		0.17	0.70	n.s.
	one vs. half or one		0.04	0.27	n.s.		0.29	0.80	n.s.
	half vs. half or one		0.02	0.34	n.s.		0.12	0.94	n.s.
	(vii) winter stage:	32				33			
	egg vs. not egg		-0.21	0.36	n.s.		-0.68	1.04	n.s.
	(viii) phenology	38	0.12	0.11	n.s.	42	0.38	0.31	n.s.
dispersal ability	(ix) wing morph:	15				8			
	short vs. long		0.18	0.28	n.s.		0.43	0.74	n.s.
	short vs. dimorphic		-0.07	0.31	n.s.		-0.17	0.77	n.s.
	long vs. dimorphic		-0.25	0.20	n.s.		-0.60	0.58	n.s.
	(x) wing load	18	-0.03	0.17	n.s.	18	-0.05	0.45	n.s.
distribution	(xi) average latitude	25	-0.05	0.23	n.s.	24	-0.21	0.64	n.s.

Summary of results for sets of top GLM models with ΔAIC<4 (95 models for "uncorrected range change", and 79 models for "corrected range change"). The importance of traits is indicated by the frequency with which they are included in the top model set (% included), and by their weighted mean coefficients, standard errors and significance levels. Results given are for minimum adequate recording effort, i.e. for "surveyed squares" with a minimum of 1 species recorded in both 1980-9 and 2000-9.

As before in the analysis with all species, results were highly consistent across all levels of recording effort and both range change measures, therefore only the results for minimum adequate levels of recording effort are presented. Residuals were normally distributed indicating that the analysis with Gaussian GLMs was robust (S 3.3 Table). There were significant results for Moran's I phylogenetic autocorrelation indices for up to about half of the top models, but index values were low throughout (S 3.4 Table). In addition, subsequent fitting of phylogenetically corrected pgls models did not change the results obtained with non-phylogenetic GLMs (S 3.7 Table), and lambda values were consistently estimated as the default minimum permitted in the pgls function, $1x10^{-6}$. We therefore concluded that the analysis with non-phylogenetically-corrected GLMs was robust.

Goodness-of-fit was drastically reduced for models that *excluded* the two species with particularly large range changes compared to models with all species: the weighted means of adjusted D^2 values were 0.12 (minimum 0.00, maximum 0.24) for both range change measures and were very similar across all levels of recording effort (S 3.6 Table).

For models with all species, despite a good average correspondence between observed and fitted range change values, there were large residuals for some species (Fig. 3.4). For models including all species, the species that had the largest positive differences between observed and fitted values (i.e. most underestimated by the models) were *Chorthippus albomarginatus, M. roeselii* and *C. discolor*; those with the largest negative differences (i.e. range changes most overestimated by the models) were *Conocephalus dorsalis*, *Chorthippus parallelus* and *Stethophyma grossum*. For models excluding *C. discolor* and *M. roeselii* the species with the largest positive differences were again *C. albomarginatus* and also *Tetrix subulata*, those with the largest negative differences were again *S. grossum* and also *Myrmeleotettix maculatus*. Results were very similar across measures of range change and levels of recording effort (S 3.8 Table).

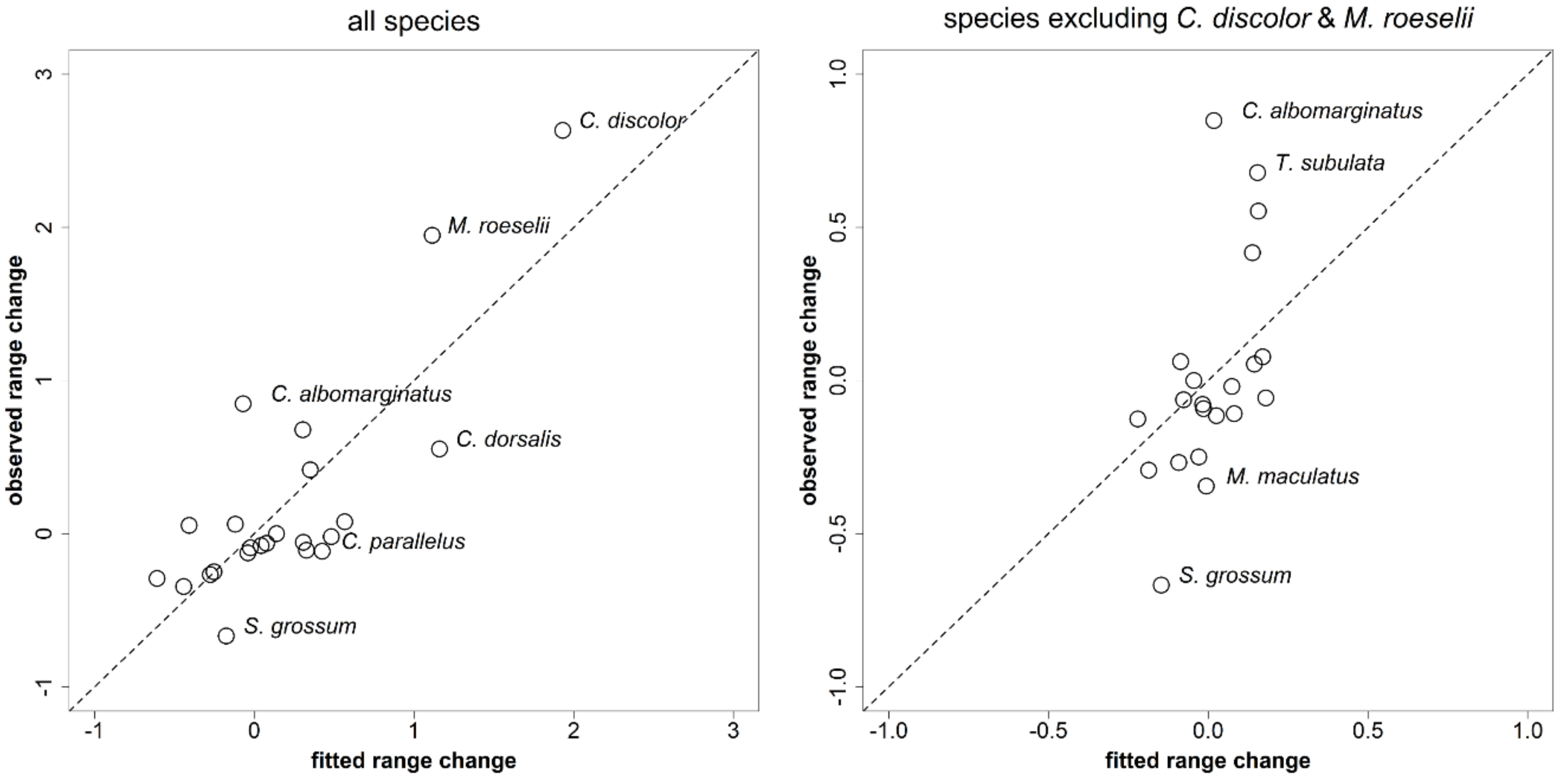


Fig. 3.4. Observed vs. fitted range change values.

Values for “uncorrected range change”, recording effort level 1. Fitted values are weighted means across the set of top GLM models with ΔAIC<4. The dashed unity line indicates equality of observed and fitted values. Species with the largest residuals have been labelled.

3.5 Discussion

Considerable distributional changes have occurred among British grasshoppers and related species in recent decades. Our analysis provides interesting indications as to which combination of traits is responsible for the particularly large range expansions of two species, *C. discolor* and *M. roeselii*. No effects were found and model fits dropped sharply when as a matter of caution these two species were omitted, and conclusions about the importance of specific traits therefore had limited relevance to the remaining species. Limited predictive and explanatory power is a common feature of traits analyses in the literature – while a number of studies find significant associations, the variation explained is generally low, and the traits that are identified for a taxonomic group may vary between studies (Simberloff 2009, Angert et al. 2011, Pocock 2011, Buckley and Kingsolver 2012, Powney et al. 2014). It is likely that characteristics of species beyond those examined explain additional variation, e.g. physiology, trophic relationships, or interactions between traits, but this remains to be demonstrated and will require more information than is currently available. For example, there is limited data on physiological tolerances and quantitative importance of food-web interactions for grasshoppers and relatives (Ingrisch and Köhler 1998, Benton 2012). Additional constraints of our study were the small number of species (23), which meant that for traits with few species in individual categories there was limited statistical power, and the necessity to employ conservative range change measures which, while robust, are unable to detect small distributional changes, or indeed more subtle changes in abundance. In the discussion of the findings of the traits analysis we restrict application mainly to *C. discolor* and *M. roeselii* because they have a dominant effect on results.

3.5.1 Range changes

Both our measures of range change, “uncorrected” and “corrected”, control for spatial variation in recording and the latter measure is also robust to overall changes in recording effort and multiple other biases (Isaac et al. 2014). Given this and the very close correlation of values across both range change measures and all levels of recording effort (Table 3.3), we are confident that they are robust, if conservative, estimates of range change.

In Britain, those grasshoppers and crickets which have restricted ranges are generally confined to the south or south-east, i.e. they are limited to the warmer and drier regions and have a range margin towards the north or north-west, presumably due to physiological constraints (Benton 2012). Consequently, where range expansions occurred, they proceeded in predominantly northerly and westerly directions. For example, this can be clearly seen in the two species with the greatest range increases in this study, *C. discolor* and *M. roeselii* (Fig. 3.5). Such north- or northwest-ward range expansions are also consistent with a climatic explanation (see discussion of average latitudes below).

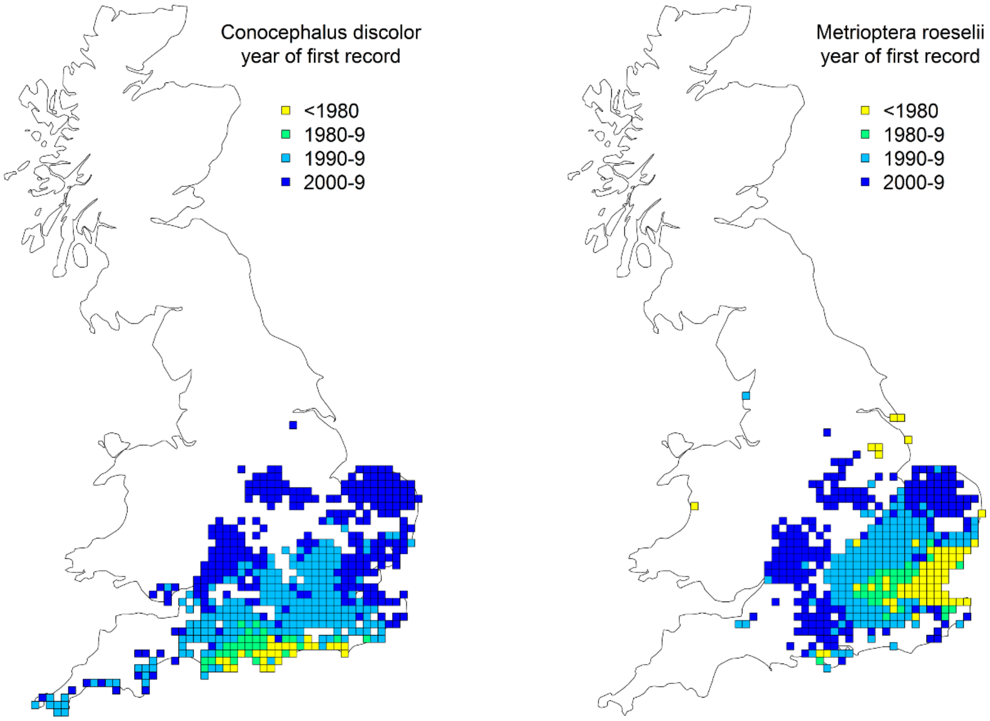


Fig. 3.5. Range expansions of Conocephalus discolor and Metrioptera roeselii in Britain between 1980 and 2009.

The figure shows years of first records of the species in each hectad. N.B.: The maps are based on the dataset retrieved from the Orthoptera Recording Scheme database for the present study (in 2013).

Populations of grasshoppers and crickets may undergo large fluctuations in density from year to year, for example in response to variations in abiotic factors such as temperature and precipitation, with densities varying by factors of up to 5 or 10 or even more between successive years (Ingrisch and Köhler 1998). These fluctuations in density may in turn lead to fluctuations in distributions, particularly at small scales (Hanski 1999). If fine-scale records of individual years were to be compared, therefore, erroneous conclusions might be reached about changing distributions. Here, we summarised records at a coarse spatial scale (10x10km squares), and examined distribution changes across whole decades (1980s vs. 2000s) (Telfer et al. 2002, Hickling et al. 2006). We are confident, therefore, that any substantial range changes observed reflect genuine change. Comparison of trajectories of change between decades with those inferred from annual series of records over the entire study period 1980-2009 confirm that large observed range changes are genuine, cumulative, and sustained and are not artefacts of one-off fluctuations or outbreaks (S 3.2 and S 3.3 Figs.).

3.5.2 Species traits

Our all-species traits analysis found three species traits to have significant effects on range changes between the 1980s and 2000s (Table 3.4). The observed significant positive effect of the number of habitats that a species utilises on its ability to extend its distribution has been documented in several species groups and is consistent with the notion that under conditions of environmental change species with a broad ecological niche are more likely to be able to find suitable resources in the landscape than specialists (Warren et al. 2001, Reinhardt et al. 2005, Gallagher et al. 2015). The species with the largest range size increases in our study, the bush-crickets *C. discolor* and *M. roeselii* are both habitat generalists occurring in many long-grass habitats. Both are likely to have benefited from "set-aside", i.e. the large areas of agricultural land left untilled in the 1990s and 2000s under farming policy, and field margins taken out of production under the subsequent "agri-environment schemes"; in addition they occur along lightly managed roadsides, railway lines and flood defences, whose linear nature may have further enhanced connectivity of suitable habitats (Gardiner 2009, Benton 2012). Potential links between the number of habitats species can exploit and climate warming are discussed below.

The second finding of our all-species traits analysis – a significant effect of oviposition site, with species which lay their eggs in vegetation increasing their ranges more than species that oviposit in the ground or at the ground-vegetation interface – may be related to land use changes and their effects on microclimates. Britain's large-scale "Countryside Survey 2007" found many indications of reduced management, and nutrient enrichment in some habitats, both in the short (since 1998/1990) and longer term (since 1978), with vegetation becoming taller, more shaded and less diverse (Carey et al. 2008). The recently published second atlas of mosses and liverworts in Britain documents particular declines for species of low-nutrient lowland habitats (Blockeel et al. 2014). Notwithstanding localised decreases in vegetation height through factors such as increasing rabbit populations (Harris and Yalden 2008) and targeted habitat management, therefore, it is possible that suitable microclimates for insects that oviposit in the ground have generally decreased, despite climatic warming. At the same time, species that oviposit in vegetation including the two with the largest range size increases in the present study, *M. roeselii* and *C. discolor*, may have benefited from climatic warming without suffering negative effects from increases in vegetation height. Conversely, the mottled grasshopper *Myrmeleotettix maculatus* has shown one of the largest declines in our study; it oviposits in the soil and is a specialist of short vegetation and bare ground exposed to the sun and is likely to be very vulnerable to succession and nutrient enrichment (Marshall and Haes 1988, Benton 2012). The importance of short vegetation or open ground for oviposition have been highlighted for other taxa such as bumblebees (Carvell 2002), butterflies (Thomas et al. 2009), moths (Fox et al. 2014) and indeed recently for grasshoppers and relatives with an explicit link to a negative effect of nutrient enrichment (Hendriks et al. 2013).

The third finding of our all-species traits analysis was a significant positive effect of low (southerly) average latitude of a species' distribution on range size. This is consistent with a positive effect of climatic warming over the study period 1980-2009: Being on their northern range edge, species with low average British latitudes such as *M. roeselii* and *C. discolor* are likely to be thermally constrained, i.e. their distributions limited by their minimum physiological requirements for warmth. Under a warming climate they are therefore expected to expand their ranges into previously unsuitable areas; such changes have been observed for multiple species groups (Perry et al. 2005, Hickling et al. 2006, Chen et al. 2011). Consistent with this explanation, *M. roeselii* and *C. discolor* have also been extending their ranges in continental Europe (Kleukers et al. 1996, Burton 2003, Poniatowski et al. 2012). There is a possibility that due to the concentration of "surveyed squares" in southern Britain (Fig. 3.1) it is easier to detect change in the more thermally limited species that occur at low average latitudes. However, it is unlikely that range changes of the magnitude observed here (in excess of 300%) would be missed even in regions with low recording intensity. In addition, expanding species would be expected to increase their distributions even away from the immediate range margin through "infill" ((Wilson et al. 2004), and see next paragraph).

An interesting aspect of species' responses to climatic warming is the interaction with habitat breadth: populations located near species' thermal limits are often confined to fewer habitats than elsewhere in their range (presumably to those which provide optimum microclimatic conditions) (Oliver et al. 2009). Climatic warming should therefore increase the range of habitats available to them ("ecological release"), and instances of this have been documented (Thomas et al. 2001, Davies et al. 2006), although other studies have failed to find such an effect, presumably because of concurrent habitat deteriorations due to other factors (Oliver et al. 2012). There is anecdotal evidence that *C. discolor* and *M. roeselii* (and the species with the third largest positive range change in our study, *Chorthippus albomarginatus*) have increased the numbers of habitats they utilise in Britain during their recent range expansions (Evans and Edmondson 2007, Benton 2012), but no specific studies have been carried out and the observed changes may be density-dependent or determined by land-use changes rather than climate-driven. Some of Britain's rarest grasshoppers and relatives are very specialised here but occur in a wider range of habitats away from the edge of their range, in continental Europe, for example the species with the largest range contraction in our study, *Stethophyma grossum* (Detzel 1998, Benton 2012). It may be that continued climatic warming will aid conservation of such species in Britain by allowing them to occupy additional habitats, but this will depend on other conditions such as moisture levels also meeting the species' requirements (Sutton 2007, 2008, Benton 2012).

Another interesting mechanism by which climatic warming could aid range expansions is through increases in voltinism (Altermatt 2010). The development of *M. roeselii* (and that of a second species which has expanded its range, *Leptophyes punctatissima*) can take either one or two years (Table 3.1): eggs laid early in the season and / or in warm parts of the species' range take one year to develop into adults, while eggs laid late or in cooler parts of the range overwinter twice before hatching (Deura and Hartley 1982, Ingrisch 1984). Increased temperatures could therefore halve generation times for parts of the populations of these species and so aid increases in numbers and range expansions. The number of generations per year is not identified as a significant trait in our analysis. This may be because the trait is too coarse to capture inter- and intra- specific *variability* in voltinism adequately: For example, *Tettigonia viridissima* ("half" a generation per year) may take two or more years to develop, and females of *Chorthippus brunneus* ("one" generation per year) exhibit seasonal and regional variability in the number of instars during development (four or five), with early and southerly eggs more likely to develop through five instars, producing larger and more fecund adults (Willott and Hassall 1998, Benton 2012). A further reason that we found no effect here may be that climatic warming may of course also aid reproduction in species such as *C. discolor* where no variation in voltinism is known to occur: warming may extend the breeding season, and increase metabolic rates and hence fecundity of adults (Willott and Hassall 1998).

In addition to the three traits discussed above, wing-length dimorphism is known to be a further very significant trait catalysing the rapid range expansion of *M. roeselii* and *C. discolor*: multiple studies suggest both species are expanding their ranges successfully through a combination of effective dispersal (aided by high numbers of macropterous individuals) and subsequent high reproductive rates (of brachypters); selection for increased dispersal at the advancing range margin appears to be reinforcing the process (Travis and Dytham 2002, Simmons and Thomas 2004, Gardiner 2009, Hochkirch and Damerau 2009, Poniatowski and Fartmann 2011c, Poniatowski et al. 2012). Wing-length is not identified as a significant predictor of range change in our analysis. Likely reasons for this include that other wing-dimorphic species have not expanded rapidly, and that our study did not take account of maximum proportions of macropters in populations, because the small total number of species did not allow a finer categorisation. In *M. roeselii* and *C. discolor* populations, macropters may reach very high proportions, while in most other wing-dimorphic species they are never more than rare (Marshall and Haes 1988, Detzel 1998, Benton 2012) and therefore presumably have little impact on rapid dispersal at the population level.

Overall, it seems likely that a *combination* of favourable traits is required for species to have been able to expand their ranges under the climatic and land-use changes of recent decades. Wing-dimorphic species such as *C. discolor* and *M. roeselii* which combine effective dispersal through large numbers of macropters with a broad ecological niche and oviposition preferences suited to recent land-use change have benefited greatly from climatic warming and expanded their range rapidly. It is instructive to compare these species to others which share some but not all of these traits: For example, *Conocephalus dorsalis* is very similar to *M. roeselii* in all three traits identified as significant in our study (Table 3.1), but has expanded its range much less (Fig. 3.2). This may be because, while wing-dimorphic, it is not known to produce large numbers of macropters (Benton 2012). A lack of information on maximum proportions of macropters in our analysis may also explain why the range change for this species is overestimated by models, while it is underestimated for *C. discolor* and *M. roeselii* (Fig. 3.4). Another species, *Chorthippus parallelus*, has somewhat less in common with *C. discolor* and *M. roeselii*: it is a habitat generalist, is wing-dimorphic and can produce very large proportions of macropters (Marshall and Haes 1988, Detzel 1998), but it oviposits in the ground and has a higher average distributional latitude (Table 3.1); the range of this species seems in fact to have declined (Fig. 3.2).

3.6 Conclusions

Long-term distributional datasets are a valuable resource that can inform research on species' responses to environmental change. Our analysis showed large changes in distributions for some grasshoppers and crickets at the scale of a whole geographical region (Britain) between 1980 and 2009, a period of extensive climatic and land use change. Range changes were positively influenced by three species traits: habitat generalism, oviposition above ground in vegetation, and a southerly distribution. However, these findings applied mainly to the two species with the greatest increases in range only, *C. discolor* and *M. roeselii*, as no effects were found for a subset of species excluding them. Several previous studies on the rapid range expansion of these two species emphasised wing-length dimorphism as the key to their success, with the ability of populations to develop large proportions of long-winged (macropterous) individuals resulting in a high phenotypic plasticity of dispersal. Our findings suggest that dispersal is not the whole picture and that it is likely to be the combination of traits that these species possess that have enabled them to thrive under recent environmental changes. Differences in their traits, however, were not significant predictors of the range size changes of the remaining individual species. We conclude that trait-based analyses may contribute to the assessment of species responses to environmental change and may provide insights into underlying mechanisms, but results need to be interpreted with caution and may have limited predictive power, particularly where trait and population trend data is not extremely detailed and species numbers are low. Advances in species distribution and abundance monitoring, and assembly of more detailed and comprehensive trait data for example alongside the collection of distribution data (Purse et al. 2012) or through follow-up investigations on the findings of studies such as the present one, will be important for future improvements in assessing the consequences of environmental change.

3.7 Acknowledgements

We are very grateful to the many volunteer recording scheme contributors who have gathered the distribution data used in this study. For statistical, R programming and other advice we would like to thank Stephen Freeman, Michael Pocock, Colin Harrower, Claire Wood, Simon Smart, Tom August, Nick Isaac, Mark Jitlal, Marco Girardello and Katie Beckmann. Many thanks to Jane Hill and Julia Ferrari for useful feedback on earlier drafts of this paper, and to two anonymous reviewers for thorough and helpful comments.

4. Environmental stochasticity is a strong determinant of colonisation rate under climate change

4.1 Abstract

Many species are undergoing extensive distributional shifts in response to climate change. Globally, further warming of 1.6-2.1°C is expected by the end of the century. A detailed understanding of species' responses to such changes is critical for conservation and adaptation, but many interspecific differences remain unexplained. One reason may be that most analyses have been based on trends in mean climate, not considering the effects of annual variation in weather, which are the conditions that individuals actually experience. For two bush-crickets (katydids) in Britain, I investigated (1) annual colonisation rates from 1977 to 2012, based on long-term distribution monitoring data, and (2) numbers of dispersive long-winged (macropterous) individuals from 2008 to 2012, based on field surveys; and related both types of data to annual variation in weather variables. Seasonal weather significantly affected colonisation rates. There were interacting effects on colonisation rates of temperature and precipitation during the period of juvenile development for both species, with colonisation highest in years when April-July weather was both warm and wet. Colonisation rate was also positively associated with warm (and dry, for *C. discolor*) August-October periods, coincident with adult dispersal and reproduction. For *C. discolor*, there was some limited evidence for similar relationships between seasonal weather and the incidence of macropterous individuals, but for *M. roeselii* there was not. The findings suggest that annual variations in seasonal weather significantly influence range expansion rates, and that the study species, and potentially others, are likely to undergo waves of expansion in climatically favourable years. A stochastic dispersal pattern might increase the overall rate of expansion by concentrating dispersal events into waves, with greater numbers of colonists increasing the likelihood of successful establishment. Weather-dependent waves of dispersal may also be advantageous in fragmented landscapes, allowing species to persist in suitable habitat patches and invest in dispersal only sporadically and under favourable conditions. Taking into account species' sensitivity to variations in seasonal weather should improve model fits to past climate-driven range changes and increase accuracy of model projections into the future. The results also highlight the importance of considering interactive effects of temperature and precipitation when examining species' responses to climate variability.

4.2 Introduction

Extensive distributional changes are being observed for many species in response to ongoing climatic changes (McCarty 2001, IPCC 2014). Rates of distribution change differ strongly between species, and while the understanding of species' responses to climate is improving, the mechanisms underlying interspecific differences often remain unclear (Hickling et al. 2006, Mair et al. 2012, Mason et al. 2015). This may be partly because most studies focus on impacts of changes in mean climatic conditions (Henry et al. 2014), particularly temperature, but neglect effects of annual variation in weather on range expansion processes, even though the latter are known to strongly affect population abundances of sensitive species (Pollard and Yates 1993, Roy et al. 2001, Wallis de Vries et al. 2011, Oliver et al. 2015b). The interactions between moisture and temperature are also rarely considered (Morecroft and Speakman 2015).

A better understanding of the effects of annual variation in weather on range expansion processes is particularly important because, in addition to further warming of 1.6-2.1°C globally by the end of the century if emissions are reduced in line with the Paris Agreement, annual and seasonal variability in the weather is predicted to increase with more frequent and greater extremes (Wolff et al. 2014, Rogelj et al. 2016). Over the same period, winter precipitation in Britain is projected to increase by 10-30%, but summer precipitation to decrease by a similar amount (Murphy et al. 2009). Such changes are likely to be detrimental to many species if they cannot move or adapt successfully, while species that can may move large distances (Thomas et al. 2004a, Thomas et al. 2006). Differential responses of species are likely to alter community composition, with significant potential implications for conservation, ecosystem function and agricultural production.

Range expansions are achieved by the combined effects of dispersal and population growth, both of which have the potential to be affected by variation in the weather. Variations in seasonal weather may strongly affect all three key stages of dispersal: emigration, transition and settlement (Clobert et al. 2012) and, in turn, affect colonisation and population persistence. Emigration from a native population is likely to be condition-dependent in many species, for example with a trigger being population densities approaching the local carrying capacity (Travis and Dytham 2012). Seasonal weather significantly influences population abundances and densities in many species (Pollard and Yates 1993, Roy et al. 2001) and is therefore likely to indirectly affect emigration in many cases, affecting both the number of potential emigrants (the source population size) and the propensity of each individual to disperse. Such effects have been investigated in “wing-dimorphic” grasshoppers and crickets, i.e. species which have two distinct morphs with radically different wing lengths (Roff 1986), making it possible to identify dispersive individuals in the field. Wing-dimorphism has been observed in many insect groups, including grasshoppers and crickets, where it occurs in a considerable proportion of species: e.g. in 25 of 166 (15%) species in central Europe, and in 7 of 32 (22%) species in Britain (Marshall and Haes 1988, Ingrisch and Köhler 1998). Such phenotypic plasticity – the development of different phenotypes from the same genotype under different environmental conditions – may be an adaptation to variable environments (Miner et al. 2005, Pigliucci 2005). In wing-dimorphic grasshoppers and crickets, development into the long-winged “macropterous” form is probably triggered primarily by high population densities during the juvenile stages, which in turn depend on factors including favourable weather such as warm temperatures (Marshall and Haes 1988, Ingrisch and Köhler 1998, Behrens and Fartmann 2004, Poniatowski and Fartmann 2009, 2011c). While plasticity influences development, individuals and populations potentially differ genetically in the environmental triggers required to stimulate development as dispersive phenotypes, and hence there is potential for evolution of increased dispersiveness at expanding range boundaries (Simmons and Thomas 2004).

The transition phase of dispersal, i.e. movement between a natal site and an individual’s destination, may also be significantly affected by weather. For example, daily movement distances of grasshoppers were found to depend strongly on maximum daily temperatures (Walters et al. 2006), and dispersal distances of thistle seeds on wind speeds (Skarpaas and Shea 2007). For species with distinct dispersal morphs these tend to be capable of much greater dispersal distances than the non-dispersive morphs; e.g. in several wing-dimorphic bush-crickets (katydids) only the long-winged morphs are able to fly, and where both morphs fly macropters are capable of significantly longer flight than the shorter-winged “brachypters” (Roff 1986, Simmons and Thomas 2004, Poniatowski and Fartmann 2011b).

Success or failure of the third phase of dispersal, settlement and establishment at a new site, can also strongly depend on weather conditions. Low initial numbers of individuals make new colonies vulnerable to stochastic extinctions through unfavourable weather, while spells of favourable weather may ensure successful establishment (Hanski 1999, Tack et al. 2015). Other factors important to this phase include species’ population dynamics at low densities, particularly the occurrence of Allee effects, i.e. negative effects of low population densities on individual fitness, including inbreeding (Kindvall et al. 1998, Travis and Dytham 2002, Lockwood et al. 2013), and species' ecological resource requirements such as habitat, and the spatial distribution of those resources (Hill et al. 2001, Clobert et al. 2012).

As ectothermic insects, grasshoppers and crickets (Orthoptera) are excellent indicators for the effects of climatic change, particularly in grasslands and other open habitats (Willott and Hassall 1998). They can also constitute a large proportion of insect biomass in grassland ecosystems, giving them particular conservation significance for example as food for threatened farmland bird species (Curry 1994, Benton 2012). In the present study I investigated effects of annual variations in seasonal weather on the rapid range expansion over recent decades of two wing-dimorphic bush-crickets (Tettigoniidae), *Conocephalus discolor* (Long-winged Conehead) and *Metrioptera roeselii* (Roesel's Bush-cricket), in Britain. Both species reach their north-western range margin in Britain: *M. roeselii* has a Eurosiberian temperate distribution, and *C. discolor* a Eurosiberian southern temperate distribution (Preston and Hill 1997, Beckmann et al. 2015). They are ecologically and biologically similar (Beckmann et al. 2015), so might be expected to have comparable responses to variations in seasonal weather.

Effects of annual variations in seasonal weather on two metrics of the range expansion process were investigated, namely: (1) annual colonisation rates of each species between 1977 and 2012, calculated from a long-term distribution monitoring dataset, and (2) numbers of long-winged (macropterous) individuals sampled in sites near the current or recent range margins, since development of macropters is likely to be the mechanism responsible for most long-distance dispersal (Vickery 1965, Meineke 1994, Simmons and Thomas 2004). I considered annual weather metrics of warmth and rainfall during the juvenile development (April to July), and adult reproduction and dispersal (August to October) periods and tested the following specific hypotheses. Numbers of macropters, and annual colonisation rates will increase with (i) warm and (ii) dry weather conditions during juvenile development, which mean warmer microclimates, speeding up growth, lowering mortality and producing higher densities (Ingrisch and Köhler 1998, Poniatowski and Fartmann 2011c, Suggitt et al. 2011). However, drought conditions during juvenile development may negatively affect the juvenile stages of sensitive insects through desiccation and adverse effects on food plant quality and vegetation structure (Ingrisch 1984, Roy et al. 2001, Oliver et al. 2015b). I therefore expected (iii) extremely low April-July rainfall to be associated with lower colonisation rates than low or intermediate rainfall. Similarly, I predicted warm temperatures during juvenile development to be particularly important in years of high rainfall and vice versa, i.e. (iv) a positive interaction between effects of warmth and precipitation: high temperatures should counteract the microclimatic cooling effects of high moisture, and high rainfall should reduce the risks of drought in hot years (Pollard and Yates 1993). I expected positive effects on colonisation rates and numbers of macropters observed at range margin sites of (v) warm and (vi) dry conditions during the adult period of reproduction and dispersal, because these are associated with higher insect metabolic rates and flight activity (Pollard 1977, Uvarov 1977).

In addition to weather effects in the same year, I expected lagged effects of weather in the previous year on macropterism and colonisation rates because high reproductive success in the parental generation may lead to higher starting densities in spring of the following year and therefore a greater likelihood of macropters developing (Gardiner 2009, Poniatowski and Fartmann 2011c). In addition, favourable weather may help populations at new sites become established, which were colonised by few individuals and remained undetected, being recorded only when numbers build up. Furthermore, eggs of *M. roeselii* (not of *C. discolor*) may take up to two years to hatch and develop into adults, depending on environmental conditions, leading to a potential lag before effects of weather become apparent in adult records (Ingrisch 1984, Benton 2012). In order to keep model complexity manageable I only investigated lagged effects for linear weather effects without an interaction, i.e. for hypotheses (i)-(ii) and (v)-(vi) only. Thus, a series of specific hypotheses were tested that all relate to the general issue of whether rates of colonisation and dispersal (morphology) vary among years, and whether these in turn depend on the prevailing and preceding climatic conditions.

4.3 Materials and Methods

4.3.1 Part 1: Effects of seasonal weather on colonisation rates

4.3.1.1 Distribution data

Distribution data were taken from the Grasshoppers and Related Insects Recording Scheme database (Orthoptera Recording Scheme 2015a, b). To date (Nov 2015), the scheme has collated some 145,818 distribution records, 10% of these being for the study species *Conocephalus discolor* and *Metrioptera roeselii*. The main aim of the scheme is to map species' distributions, and records are mostly gathered without any standard protocol or measure of recording effort. These are 'presence only' data and there is no indication of whether a location without records was occupied or not. This lack of absence records prohibits the use of conventional site-occupancy models to study colonisation (MacKenzie et al. 2002, MacKenzie et al. 2003).

The range expansion of *C. discolor* and *M. roeselii* in mainland Britain was analysed over the 36-year period 1977 to 2012. These years were selected because the recent range expansion of the two species was first recorded around 1977 (Marshall and Haes 1988, Simmons and Thomas 2004), and 2012 is the final year during which field data were collected in the current study (see below). Data were summarised at a 10km grid square ("hectad") resolution, based on the British National Grid.

All calculations were performed in the statistical software environment "R", version 3.2.2 (R Core Team 2015).

4.3.1.2 Quantifying annual colonisation rates

Annual colonisation rates were estimated in the following steps, which aim to minimise biases due to (i) temporal and spatial variation in recording effort, (ii) changes in the size of the source population and (iii) the area available for colonisation within a typical maximum dispersal distance each year (which varies as distributions expand and change shape):

- The typical maximum dispersal distance for each species across the study period was quantified by computing the 95th percentile of the distances between any newly recorded ("colonised") hectad and the nearest hectad with a previous record for that species. Distances were taken between hectad centres. Analyses were repeated with the 90th percentile in order to test sensitivity to this arbitrary cut-off. A cut-off was used to exclude unusually large dispersal distances arising from accidental transport by humans (Kaňuch et al. 2013) as opposed to natural dispersal.

- For a given year *t* the previously known distribution was extracted, i.e. hectads with a record for the species up to year *t-1* (grey squares in Fig 4.1)
- Around this distribution, hectads falling within the “typical maximum dispersal distance” were identified (white squares)
- Of these squares, those were identified that were “surveyed” in year *t*, i.e. had at least one record of any of the Orthopteran species that occur in Britain (squares marked by “x”)
- Finally, I calculated the proportion of these “surveyed squares within the typical maximum dispersal distance” that were recorded as colonised, i.e. had a record for the study species in year *t* (red “+”). Squares colonised beyond the typical maximum dispersal distance (blue “+”) were by definition few and not counted in year *t*; in subsequent years, however, they were included in the “previously known distribution”, i.e. considered as potential source populations for colonisations.
- This “proportion of the surveyed squares colonised within the typical maximum dispersal distance” was defined as the annual measure of colonisation rate (ratio of red “+” to black “x”).

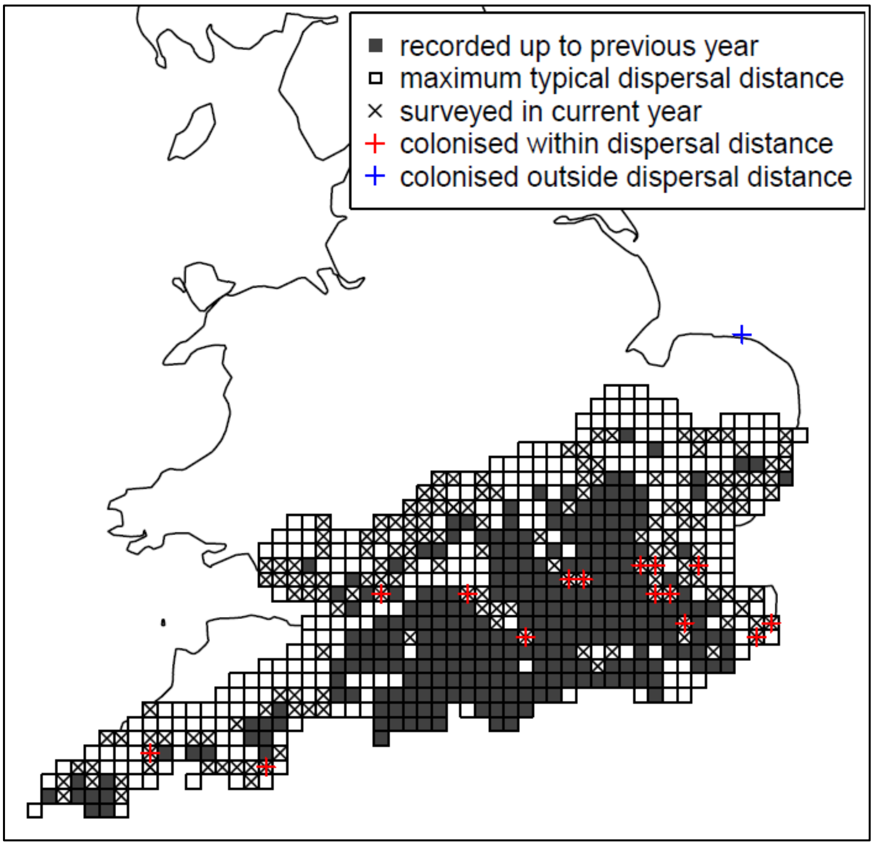


Fig 4.1. Calculation of annual colonisation rate, using *Conocephalus discolor* in the year 2000 as an example.

Colonisation rate for each year was calculated as the proportion of the previously unoccupied surveyed squares within the typical maximum dispersal distance that were colonised (ratio of red “+” to black “x”).

4.3.1.3 Weather data and definition of seasonal weather variables

Seasonal weather variables were derived from the Centre for Ecology and Hydrology’s “CHESS” dataset (Robinson et al. 2015). The monthly averages for the “Lowland England” biogeographical region were used, whose extent encompasses the current distributions of the study species. The following two variables were calculated:

(1) Monthly warmth, measured as growing degree days above 10°C (GDD10). GDD have been widely used as a measure of the sum of warmth above a threshold temperature T_{base} above which the biological processes of interest occur. An individual day’s GDD are calculated as any positive difference between the average daily temperature and this threshold:

$$GDD = ([T_{max} + T_{min}] / 2) - T_{base}$$

where T_{max} and T_{min} are the daily maximum and minimum temperatures and set to T_{base} when they are less than T_{base} (McMaster and Wilhelm 1997). A value of 10°C was used for T_{base}: no exact values have been determined for a minimum temperature above which larval development commences for the two study species, but 10°C is a typical value for other European Orthoptera (Ingrisch and Köhler 1998), and is the lower temperature threshold for development of *C. discolor* in an unpublished experiment (Delf 2013). No upper threshold was used in the GDD calculation because the maximum temperatures for the Lowland England region did not reach the maximum of 32-40°C typically tolerated by European Orthoptera (Ingrisch and Köhler 1998). Average daily GDD values were summed across the days in each month to produce a monthly total.

(2) Monthly rainfall. The CHESS dataset provides average rainfall in kg per m^2 per second which was multiplied by the number of seconds in a day (86,400), and the number of days for each month to give total monthly rainfall in kg per m^2, equivalent to the familiar mm of precipitation (i.e. 1 kg/m^2 = 1 mm).

The above monthly variables were summed for April to July of each year to characterise weather conditions during the main period of juvenile development of the study species, and for August to October to describe conditions during reproduction and dispersal (Benton 2012). I analysed effects of weather variables on colonisation rates in the same year, as well as effects of weather in the previous year (parental generation). There was therefore a total of eight main weather variables: GDD10 and rainfall sums for April to July, and August to October, for the same and the preceding years (S 4.1 Table). In addition to weather variables, calendar year was included as a variable in order to account for any overall trend in colonisation rate over time independent of annual weather conditions, for example due to long-term changes in land use, vegetation structure, or evolution of dispersal ability (Beckmann et al. 2015).

In order to test the hypothesis that intermediate or low April to July rainfall was more beneficial than very low rainfall, a quadratic term for April to July rainfall was also included. Similarly, to investigate the prediction that warm temperatures were particularly important in years of high rainfall during April to July, an interaction term between rainfall and GDD10 was included.

4.3.1.4 Model fitting, selection and averaging

First, collinearity between explanatory variables was examined using pair-wise Pearson's correlation coefficients. No problematic correlations were found with $|r| < 0.5$ in all cases.

Effects of seasonal weather on annual colonisation rates were investigated by assuming that the proportion of squares colonised in year t (C_t) was binomially distributed ($C_t \sim Bin\ [S_t, p_t]$ where S_t is the number of surveyed squares in year t and p_t the colonisation probability). I fitted binomial Generalised Linear Models (GLMs) with a logit link function relating colonisation probability to predictors. Rather than selecting a single optimum model a multi-model inference approach was taken. GLMs were fitted for all combinations of the predictors, with the quadratic and interaction terms for April to July rainfall only included together with the corresponding main effects, a total of 1,023 initial models. Models whose Akaike information Criterion (AIC) value fell within 4 units of the model with the lowest value were then selected as the set of top models that had considerable statistical support (Akaike 1974, Burnham and Anderson 2002). The relative importance of each variable was then calculated as the percentage of top models in which they occurred, and coefficients were averaged across top models using Akaike weights (Burnham and Anderson 2002, Wagenmakers and Farrell 2004). Similarly, weighted mean standard errors (SE) of each coefficient b were calculated according to the following formula derived from (Burnham and Anderson 2002):

$$SE(b_{all}) = \sum_{i=1}^{n} w_i \sqrt{[SE(b_i)]^2 + [b_i - b_{all}]^2}$$

n being the number of retained models, w_i the Akaike weight of model i, $SE(b_i)$ the standard error of coefficient b in model i, and b_{all} the weighted mean of all estimates of coefficients b across the n models. Akaike weights were scaled so that their sum equalled 1 for each predictive variable, i.e. w_i values were divided by the sum of Akaike weights of all models which included the variable whose SE was to be calculated. Confidence intervals (CI) were then calculated by multiplying weighted mean SEs by factors of 1.645 (90% CI), 1.96 (95% CI), 2.58 (99% CI) and 3.29 (99.9% CI) and adding / subtracting them from weighted mean coefficients. Predictors were considered to be significant if their confidence intervals did not span zero.

To assess model fits, weighted mean fitted values of top models were plotted against the residuals from the weighted means, and against observed values. As a measure of overall fit of top models, ratios of residual deviance to degrees of freedom were calculated.

4.3.1.5 Sensitivity analysis

I tested the sensitivity of my conclusions to the way the analyses were performed in three ways:

Firstly, the cut-off point for the calculation of the “typical maximum dispersal distance” for each species was changed from the 95th to the 90th percentile of the dispersal distances across all sites and years.

Secondly, I examined whether consistent results were obtained with a shorter study period (1988 to 2012) that excluded the initial years of slow range expansion and all years with zero recorded hectad colonisations, covering only the years of continuous, positive range expansion.

Thirdly, the definition of colonisations was changed: where in the first instance only the first record for each square was defined as a colonisation, i.e. no extinctions and re-colonisations were assumed to occur, it was now assumed that populations went extinct if not recorded in a hectad during four years of “visits”, i.e. during four years in which any other Orthopteran species was recorded in the square, analogous to the definition of extinction used in the UK Butterfly Monitoring Scheme (Pollard and Yates 1992). A record for the study species after such an extinction was considered a renewed colonisation.

4.3.2 Methods Part 2: Effects of seasonal weather on incidence of long-wingedness

4.3.2.1 Field survey

Eleven field sites were surveyed annually from 2008 to 2012 and the numbers of macropterous and brachypterous individuals of *C. discolor* and *M. roeselii* counted, with *C. discolor* recorded at between 7 and 11 of these sites and *M. roeselii* at 4 to 5 sites annually (Fig 4.2, S 4.2 and S 4.3 Tables). For each species, sites were selected which were either newly colonised (first recorded in the Orthoptera Recording Scheme database in the 2 years prior to 2008), or surveyed in a previous study in 2000-1 (Simmons and Thomas 2004) and lay at the species' range margin then (first recorded in the 9 years prior to 2000). In order to conduct field work efficiently, where possible sites were selected where both species occurred together.

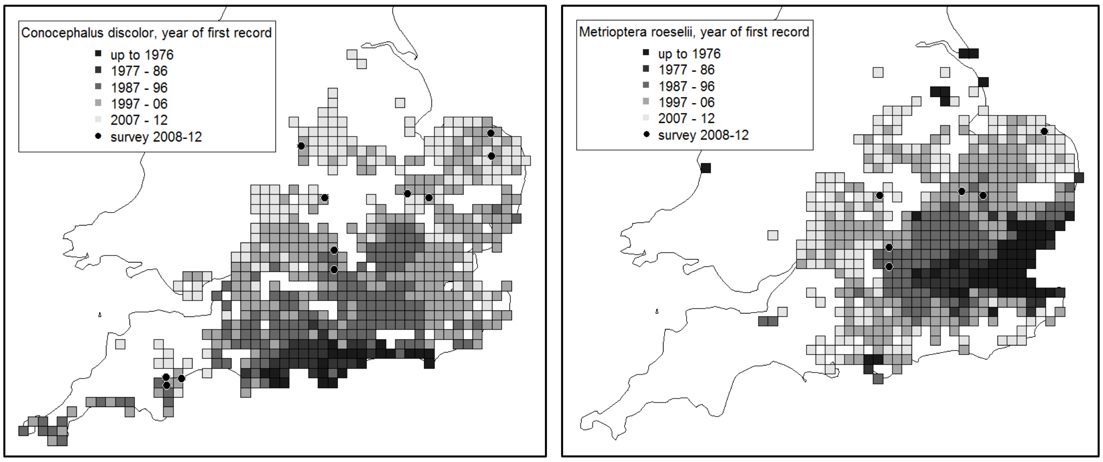


Fig 4.2. Location of 2008-2012 field survey sites in the context of the expanding distributions of the study species in southern Britain.
Species distribution squares are shaded according to the year of the first record to illustrate the species' substantial range expansions over recent decades.

Surveys were conducted between mid-July and mid-October, the time when adults of *C. discolor* and *M. roeselii* are active (Evans and Edmondson 2007). During each visit, as many adult individuals as possible were recorded for each species. Individuals of *M. roeselii* were recorded as brachypterous when their wings did not reach the end of the abdomen, and macropterous where their wings extended beyond the end of the cerci: this visual assessment of wing morphology was found to be 100% reliable in a previous study (Simmons and Thomas 2004). For *C. discolor* brachypterous insects were those with wings not extending beyond the cerci; insects with wings extending to the end of the ovipositor or beyond in females, or an equivalent length in males, were recorded as macropterous. Any *C. discolor* individuals with intermediate wing lengths were caught and wing and body lengths measured with callipers to a precision of 0.1mm, and subsequently wing morphs were assigned using an equation derived in a previous study with the cut-off line between wing morphs defined as:

$$\textit{wing length} = 1.818 + 0.898 * \textit{body length}$$

Individuals with wing lengths above this cut-off were categorised as macropterous, with shorter wings as brachypterous (Simmons and Thomas 2004, Simmons 2015). In a few instances, two visits were performed to a field site in a year; to avoid problems with pseudo-replication only the visit with the most similar date to visits to the site in other years was used in the present analysis.

4.3.2.2 Definitions of seasonal weather variables and other covariates

The same eight seasonal weather variables were calculated for each field site and visit as for the analysis of distribution data (see above), but using the local 1km square data from the CHESS dataset instead of the lowland England regional averages: sums of warmth (GDD10) and rainfall (mm) for April-July and August-October for each study site and year of visit and the preceding year. As before, a quadratic term for April to July rainfall and an interaction between April to July rainfall and warmth was included.

To characterise the colonisation history of study sites, their distance from the range core was calculated, defined as the distance in km between the centre of the 10 km square in which the field site was located and the centre of the nearest 10 km square with a record for the species up to and including the year 1976, before the recent range expansions began (Marshall and Haes 1988, Simmons and Thomas 2004). For each field visit the recorded population density of the study species was calculated, defined as the number of individuals seen per site divided by the length of the visit in minutes. At sites with both species, half the time was allotted to searching for each species and the visit length was therefore divided by 2 to calculate densities.

Three sources of potential sampling bias were accounted for by including the following variables in analyses: (1) day of year, i.e. the Julian day on which the visit occurred; (2) time of day, defined as the proportion of the period of daylight hours between sunrise (= 0) and sunset (= 1) on which the visit was centred. Sunrise and sunset times for each site and visit date were compiled from (Thorsen 2014). (3) mean temperature of the day for each field visit, extracted from the 1km gridded CHESS dataset (S 4.2 and S 4.3 Tables).

4.3.2.3 Model fitting, selection and averaging

To investigate the effects of annual weather and potential sampling biases on proportions of macropterous individuals in year t at site s (M_{ts}) these were assumed to be binomially distributed ($M_{ts} \sim Bin\ [I_{ts}, p_{ts}]$ where I_{ts} is the number of individuals surveyed and p_{ts} the probability of individuals being long-winged). I fitted binomial generalized linear mixed models (GLMMs) with a logit link function relating probability to predictors with survey site as a random effect, using the “glmer” function in the R package “lme4” (Bates et al. 2015). To select optimum models and infer results across them I took the same model averaging approach as for the analysis of distribution data (see above). I started with GLMMs for all combinations of predictive variables, with the quadratic and interaction terms for April to July rainfall only included together with the corresponding main effects. I limited combinations to a maximum of 6 variables per model, because larger numbers of predictors led to some model convergence failures. For the same reason, all predictors were centred on 0 by subtracting their mean (Quinn and Keough 2002), and the quadratic term for April-July rainfall was scaled by a factor of 0.001 in order to bring its values onto a similar scale to the other weather variables. There was an initial total of 5,188 models for each species from which sets of optimum models were selected using AIC as above.

4.3.2.4 Correlations between predictors

Standard measures of correlation are not adequate for nested data as in my case, where weather varied by year, and within years by field site (Dormann et al. 2013). To identify potential collinearity between explanatory variables I therefore considered correlations between fixed effects estimated in the GLMMs (S 4.4a+b Tables) (Bates et al. 2015).

4.4 Results

4.4.1 Part 1: Effects of seasonal weather on colonisation rates

4.4.1.1 Maximum typical dispersal distances

Between 1977 and 2012, a total of 559 hectads were recorded as colonised by *Conocephalus discolor*, and 455 by *Metrioptera roeselii* (excluding re-colonisations following extinctions, see sensitivity analysis below). Colonisation distances, i.e. distances to the nearest previously occupied squares, ranged from the minimum of 10km (adjacent squares) to a maximum of 216km for *C. discolor* and 166km for *M. roeselii*. As is typical for dispersal distance kernels (Nathan et al. 2012), the distribution of dispersal distances was strongly left-skewed with small values predominating (Fig 4.3). For both species, the median colonisation distance was 10km and the upper quartile was 14.1km (diagonally adjacent), i.e. over 75% of colonised squares were adjacent to at least one square with a previous record for the species. The 95th percentile of colonisation distances, defined as the “maximum typical dispersal distance” for subsequent calculations, was 31.6km for *C. discolor* and 28.8km for *M. roeselii*.

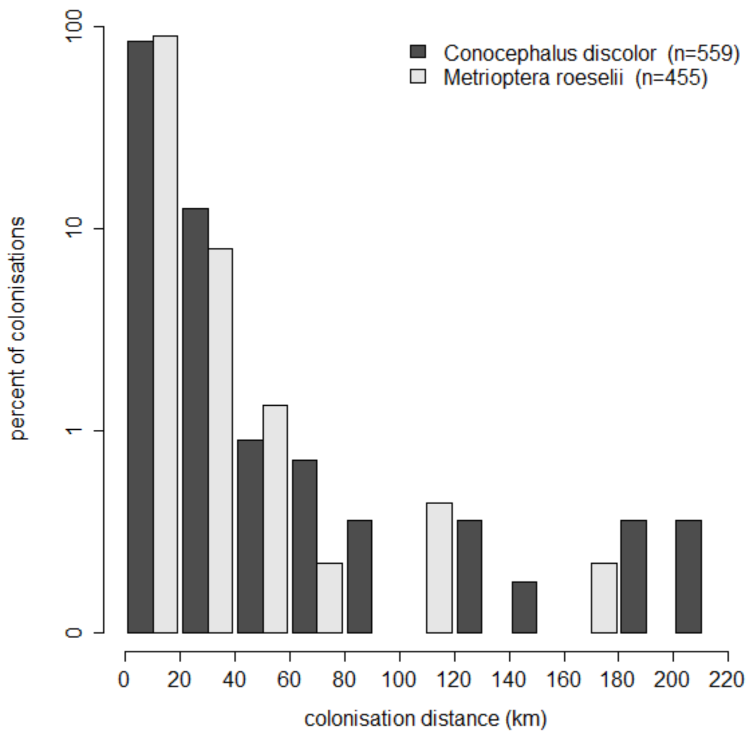


Fig 4.3. Histogram of colonisation distances for *Conocephalus discolor* and *Metrioptera roeselii* between 1977 and 2012.

Colonisation distance was defined as the distance between the centroid of a newly recorded hectad and the centroid of the nearest hectad with a previous record for the species. Histogram intervals include their right-hand endpoint, but not their left one, e.g. the first bars include colonisation distances > 0 km and ≤ 20 km. Note log scale of y-axis.

4.4.1.2 Annual colonisation rate

Over the study period 1977-2012, the distribution of *C. discolor* increased from 22 to 567 occupied hectads, and that of *M. roeselii* from 58 to 495. Annual numbers of surveyed hectads colonised within the maximum typical dispersal distance for *C. discolor* ranged from 0 to 54 (median 12.5), and for *M. roeselii* also from 0 to 54 (median 11). These numbers of squares were then converted to proportions of surveyed squares colonised (to take account of annual variation in recording effort). They equate to proportional colonisation rates of 0 to 0.40 (mean 0.15, standard deviation 0.09) for *C. discolor* and 0 to 0.45 (mean 0.12, standard deviation 0.10) for *M. roeselii* (S 4.5 Table). Thus, colonisation rates varied from zero to 40% or more, depending on the year.

4.4.1.3 Effects of seasonal weather

Several weather parameters were included in large proportions of top models and had significant effects on recorded colonisation rates (Table 4.1, left half). For both *C. discolor* and *M. roeselii*, there was a significant positive interaction in 100% of top models between the effects of April-July warmth and rainfall (squared) in the year of colonisation. These therefore have to be interpreted in conjunction; together they suggest that colonisation rates increased significantly for both study species when April to July sums of both warmth and rainfall were high, contrasting with little or no increase if either weather parameter was low (and even a slight decrease in colonisation rates with increasing temperatures under dry conditions for *M. roeselii*) (Fig 4.4). For *C. discolor*, there was also a near-significant ($p<0.1$) positive effect of April to July rainfall of the preceding year. Colonisation rate for both species was positively affected by high sums of August to October warmth in the year of colonisation (100% and 91% of top models respectively). There were differing effects for August to October rainfall, with high values in the previous year affecting colonisation rates of *C. discolor* negatively, but *M. roeselii* apparently benefiting from high rainfall in the year of colonisation (but see results of sensitivity analysis below suggesting the latter result is not robust). For *M. roeselii*, there was a significant positive effect of year, i.e. a significant overall increase in colonisation rate over time, over and above the effects of weather, which was not apparent for *C. discolor*.

Table 4.1. Effects of seasonal weather on annual colonisation rate and incidence of long-wingedness in *Conocephalus discolor* and *Metrioptera roeselii*

			Effects on colonisation rate (1977-2012)								Effects on incidence of long-wingedness (2008-12)							
			Conocephalus discolor				*Metrioptera roeselii*				*Conocephalus discolor*				*Metrioptera roeselii*			
			% included	weighted mean coefficient	weighted mean standard error	sig	% included	weighted mean coefficient	weighted mean standard error	sig	% included	weighted mean coefficient	weighted mean standard error	sig	% included	weighted mean coefficient	weighted mean standard error	sig
(Intercept)			100	-8.6387	11.5205		100	-85.4484	16.2668		100	-3.4147	0.2979		100	-3.2857	0.3307	
warmth (GDD10)	**April-July**	**same year**	100	-0.0017	0.0023		100	-0.0060	0.0030	*	67	0.0117	0.0065	.	72	-0.0297	0.0138	*
		previous year	36	-0.0009	0.0014		41	-0.0005	0.0016		60	-0.0154	0.0084	.	31	-0.0212	0.0144	
	August-October	**same year**	100	0.0057	0.0014	***	91	0.0039	0.0015	*	60	0.0195	0.0100	.	30	-0.0239	0.0170	
		previous year	32	-0.0006	0.0013		64	0.0024	0.0015		10	0.0013	0.0088		18	-0.0087	0.0106	
rainfall (mm)	**April-July**	**same year**	100	-0.0152	0.0052	**	100	-0.0272	0.0065	***	19	0.0027	0.0034		100	0.0048	0.0392	
		same year, squared	100	-2.19E-05	1.39E-05		100	-1.63E-05	1.58E-05		0	-	-		35	-0.1313	0.0947	
		previous year	52	0.0020	0.0012	.	50	0.0015	0.0014		96	0.0078	0.0032	*	42	-0.0183	0.0098	.
	August-October	**same year**	52	-0.0015	0.0010		77	0.0026	0.0012	*†	33	-0.0050	0.0041		14	-0.0013	0.0116	
		previous year	96	-0.0022	0.0010	*	41	-0.0011	0.0010		46	-0.0096	0.0045	*	14	0.0096	0.0127	
interaction of warmth and rainfall (April-July, same year)			0	-	-		0	-	-		10	1.20E-04	7.24E-05		11	5.61E-05	8.42E-05	
interaction of warmth and rainfall squared (April-July, same year)			100	1.41E-07	3.99E-08	***	100	1.73E-07	5.04E-08	***	0	-	-		0	-	-	
year			44	0.0091	0.0082		100	0.0433	0.0085	***	n/a				n/a			
day of year			n/a				n/a				8	-0.0025	0.0130		21	-0.0108	0.0105	
time of day			n/a				n/a				10	-1.1509	1.3457		63	3.3614	1.8655	.
mean temperature			n/a				n/a				8	-0.0008	0.0811		53	0.1615	0.0939	.
population density			n/a				n/a				100	-7.6205	2.3051	***	25	1.7156	1.4670	
distance from core			n/a				n/a				15	0.0047	0.0056		10	-0.0066	0.0123	

Left half: Summary of results for GLMs with ΔAIC < 4 (a set of 25 top models for *C. discolor* and 22 for *M. roeselii*). Results are for the time period 1977 to 2012. Colonisations up to the 95th percentile of dispersal distances were considered ("typical maximum dispersal distance" of 31.6 km for *C. discolor* and 28.8 km for *M. roeselii*).

Right half: Summary of results for GLMMs with ΔAIC < 4 (a set of 52 top models for *C. discolor* and 148 for *M. roeselii*). Field surveys of numbers of macropters were carried out in 2008-2012.

The importance of variables as predictors is indicated by the proportion of top models in which they are included (% included), and by their coefficients and standard errors (weighted means across top models) and associated significance levels (sig: . = $p<0.1$, *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$). Note that main effects involved in significant interactions are also significant, and interacting effects have to be interpreted together (Fig 4.4). † The positive effect of August-October rainfall on colonisation rate of *M. roeselii* was not robust in a sensitivity analysis and is not considered reliable.

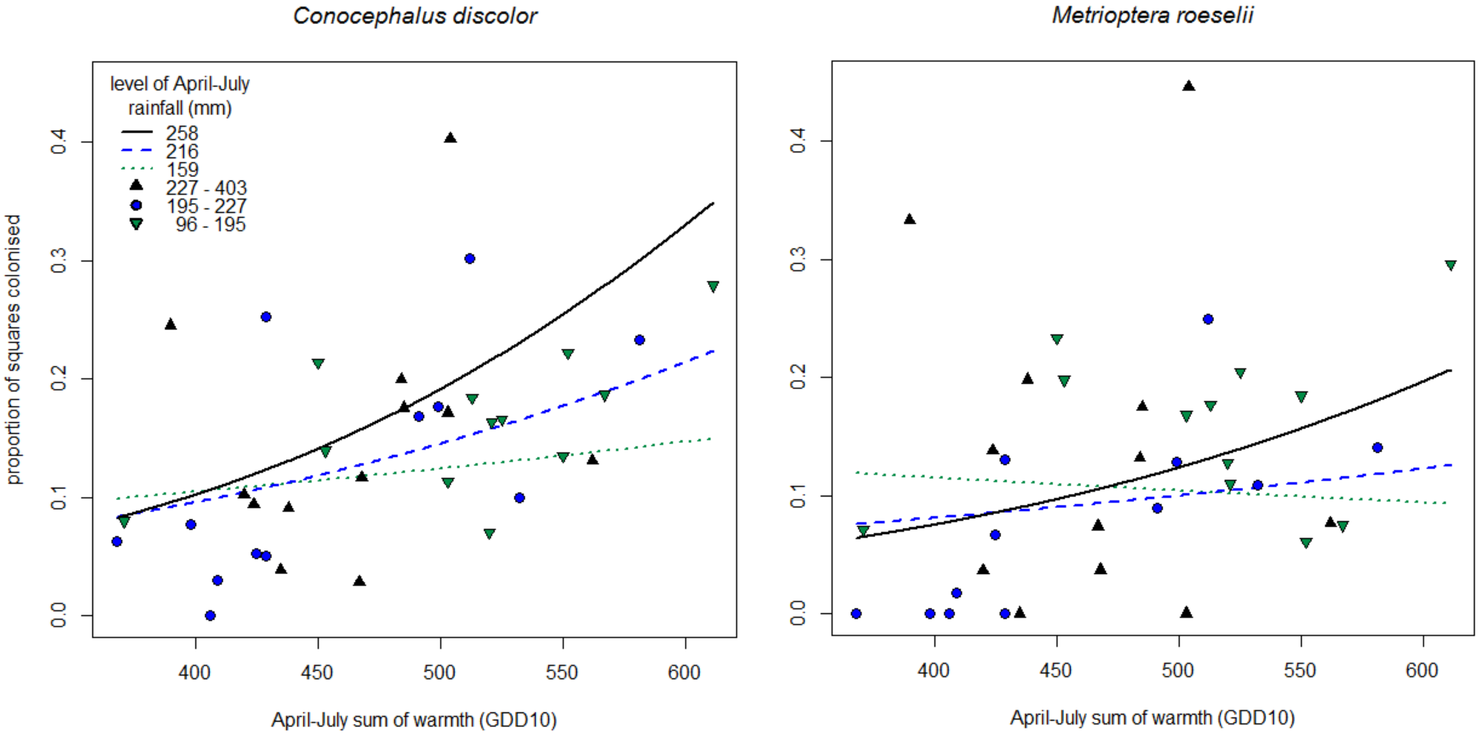


Fig 4.4. Interacting effects of April to July warmth and rainfall in the study year on colonisation rates of *Conocephalus discolor* and *Metrioptera roeselii*. Lines show effects of warmth predicted in top models for three different levels of rainfall: the 1st (dotted green line), 3rd (dashed blue line) and 5th (solid black line) sextiles of sums of April to July rainfall. Symbols show data points, with symbol type and colour indicating three levels of rainfall which broadly correspond to the three modelled lines: minimum to 2nd sextile (green triangles pointing down), 2nd to 4th sextile (blue circles) and 4th sextile to maximum (black triangles pointing up) of sums of April to July rainfall. (Note, however, that the interaction is modelled on all data points together, and the division into 3 levels of rainfall here is for illustrative purposes only). Sums of warmth (x-axis) range from the minimum to the maximum values in 1977-2012. Values for all other predictive variables were set to their means. Plots are for the first in the sets of top models (ΔAIC=0).

Sets of top models with ΔAIC < 4 contained 25 models for *C. discolor* and 22 models for *M. roeselii*. Fitted values were very consistent across top models for each species (Fig 4.5, top), and plots of observed vs. fitted values showed no large deviations from the unity line (Fig 4.5, bottom). Plots of residuals vs. fitted values did not show any patterns, and the average ratio of residual deviance to degrees of freedom across top models was 1.94 for *C. discolor* and 3.94 for *M. roeselii*, indicating a moderate degree of overdispersion (S 4.6 Table, and see section 4.5.1.2).

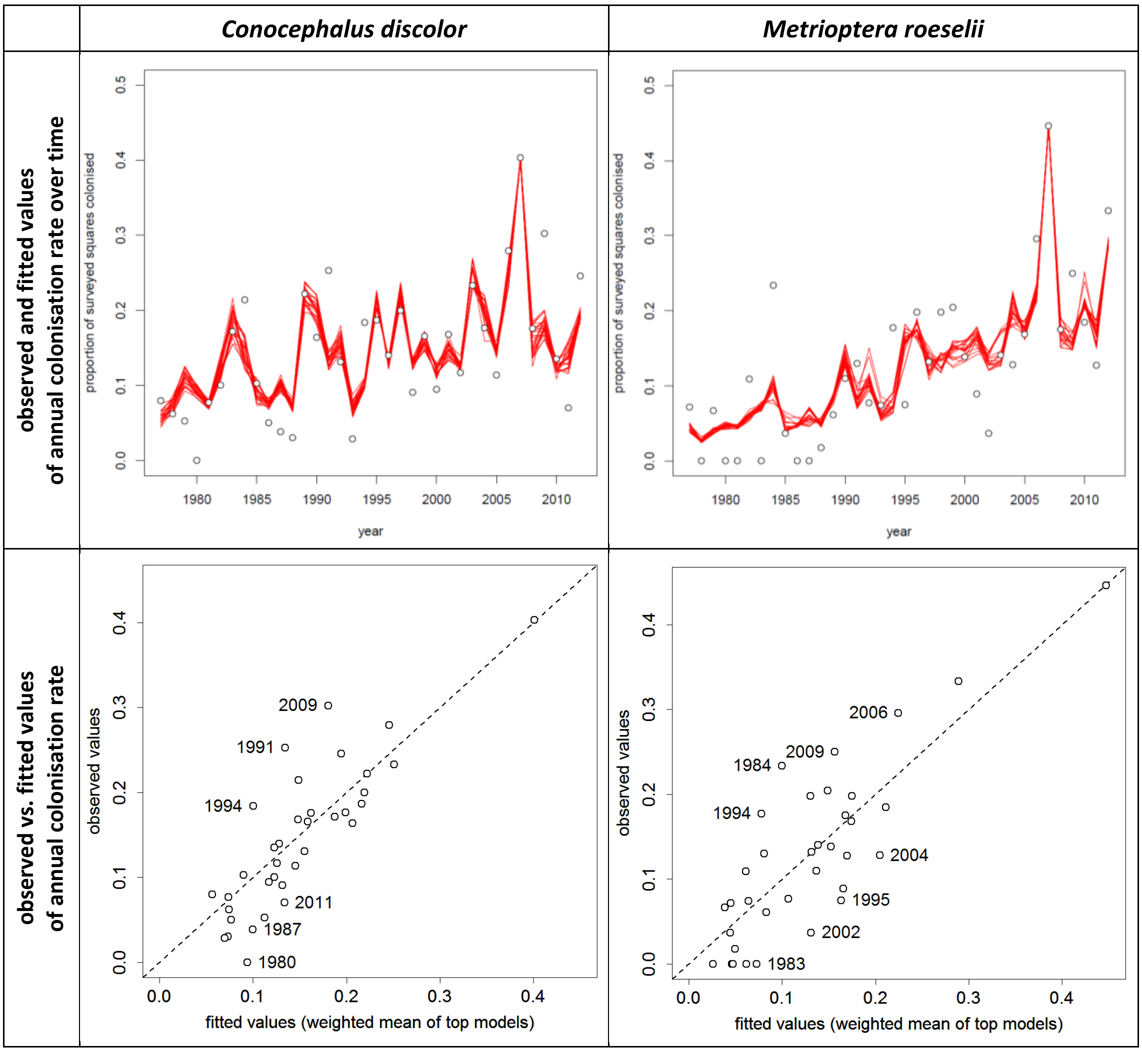


Fig 4.5. Observed and modelled values of annual colonisation rate.

Top: Plots of observed and fitted values of annual colonisation rate over time. Circles indicate observed values of the proportion of surveyed squares within the “maximum typical dispersal distance” that were colonised; lines indicate the fitted values of top models with ΔAIC < 4 (25 models for *C. discolor*, 22 models for *M. roeselii*).

Bottom: Observed vs. fitted values of annual colonisation rate. Fitted values are weighted means across sets of top models with ΔAIC < 4. Dashed lines indicate equality of observed and fitted values. Years with the largest residuals are labelled.

4.4.1.4 Sensitivity analysis

A change in the cut-off for colonisation distances from the 95th to the 90th percentile resulted in a large reduction of the assumed "typical maximum dispersal distance" from 31.6 to 23.5km for *C. discolor* and from 28.8 to 21.4km for *M. roeselii*. Results of the analysis of weather effects on colonisation were robust to this change. For both species all the same variables had significant effects and in the same direction of impact as before (S 4.7 Table).

Weather effects on colonisation were also mostly robust to a change in the start year of the analysis from 1977 to 1988, with the same significant effects identified in the sets of top models as before for both species, except August to October rainfall in the year of colonisation for *M. roeselii* (S 4.8 Table). The coefficient of *year* for *M. roeselii* was little changed, despite the deletion of several years with zero recorded hectad colonisations between 1977 and 1988 (cf. Fig 4.5).

When hectads were assumed to go extinct if not recorded in 4 years of visits (Pollard and Yates 1992) the colonisation data for both study species changed considerably, but the findings of weather effects on colonisation were again largely robust to these changes. Over the study period 1977-2012 there were a total of 155 possible hectad extinctions for *C. discolor* (between 0 and 18 annually, median 3), and a total of 95 for *M. roeselii* (between 0 and 11 annually, median 2). This meant smaller source populations from which (re-) colonisations were assumed to have occurred, and median annual population size for *C. discolor* was 113.5 hectads, compared to a median of 124.5 hectads without the assumption of extinctions; median for *M. roeselii* was 124 compared to 142 without extinctions (S 4.5 Table). Similarly, it meant larger numbers of colonisations, since records for squares that had gone extinct were now assumed to be re-colonisations: the median annual number of surveyed hectads colonised for *C. discolor* was 14 (without extinctions 12.5) and for *M. roeselii* 13.5 (without extinctions 11). The 95th percentile of colonisation distances remained at 31.6km for *C. discolor* and decreased slightly from 28.8 to 28.3km for *M. roeselii* (S 4.1 Fig). Mean colonisation rates remained at 0.15 for *C. discolor* and increased from 0.12 to 0.14 for *M. roeselii*. The same weather variables affected colonisation rates as before for both species, with the exception of August to October rainfall in the year of colonisation for *M. roeselii*, which was no longer significant (S 4.9 Table).

Overall, the analyses and interpretation were not sensitive to the assumed typical maximum dispersal distance, to the start date, or to assumptions about extinction and re-colonisation in both species. However, for *M. roeselii,* the effect of August to October rainfall in the year of colonisation was sensitive to the latter two and therefore, is not a reliable predictor variable for this species.

4.4.2 Results Part 2: Effects of seasonal weather on incidence of long-wingedness

4.4.2.1 Field survey

From 2008 to 2012, *C. discolor* was surveyed at 7 to 11 sites, and *M. roeselii* at 4 to 5 sites (Fig 4.2). *M. roeselii* was recorded at only two newly colonised sites, and at one of these in only one year (S 4.3 Table). Total numbers of surveys (i.e. sample sizes for subsequent analyses of weather effects) were 46 for *C. discolor* and 23 for *M. roeselii*. Numbers of individuals recorded per visit ranged from 1 to 58 (median 21.5) for *C. discolor* and from 1 to 59 (median 24) for *M. roeselii*. Proportions of long-winged individuals (macropters) ranged from 0 to 0.35 (mean 0.03) for *C. discolor* and from 0 to 0.18 (mean 0.04) for *M. roeselii* (S 4.2 and S 4.3 Tables).

4.4.2.2 Effects of seasonal weather

Proportions of dispersive long-winged individuals of *C. discolor* were positively associated with April to July rainfall of the preceding year (included in 96% of top models), and there was a significant negative effect on macroptery of August to October rainfall of the preceding year (46% of top models) (Table 4.1, right half). These effects agreed with equivalent significant ($p < 0.05$) or near-significant ($p < 0.1$) effects of seasonal weather on colonisation rates for *C. discolor* (Table 4.1, left half). There were near-significant positive effects of warmth in April to July (67% of top models) and August to October (60%) of the study year on incidence of observed macropters in *C. discolor*; these agree with corresponding significant weather effects on colonisation rates, although there was no evidence for an interaction between the effects of April to July warmth and rainfall on macropterism (10% of top models). There was a near-significant negative effect of April to July warmth of the preceding year (60%), which did not have an equivalent among weather effects on colonisation rates. In addition to weather effects, there was a significant negative association between population density and incidence of macroptery for *C. discolor* (included in 100% of top models).

Only one significant effect was observed for *M. roeselii*: a negative association of April-July warmth in the study year with numbers of long-winged individuals (72% of top models). There was no evidence for an interaction of this effect with warmth during the same period (11%). There were near-significant positive effects of the time of day (63%) and mean temperature of the day of field visits (53%) on observed proportions of macropters, and a near-significant negative effect of April to July rainfall of the preceding year (42%).

The analysis produced 52 top GLMM models with ΔAIC < 4 for *C. discolor* and 148 top models for *M. roeselii*, with plots of residuals vs. fitted values not showing any strong patterns, and plots of observed vs. fitted values showing no large deviations from the unity line (Fig. 4.6). The average ratio of residual deviance to degrees of freedom across top models was 2.85 for *C. discolor* and 3.17 for *M. roeselii*, indicating a moderate degree of overdispersion (S 4.6 Table, and see section 4.5.1.2).

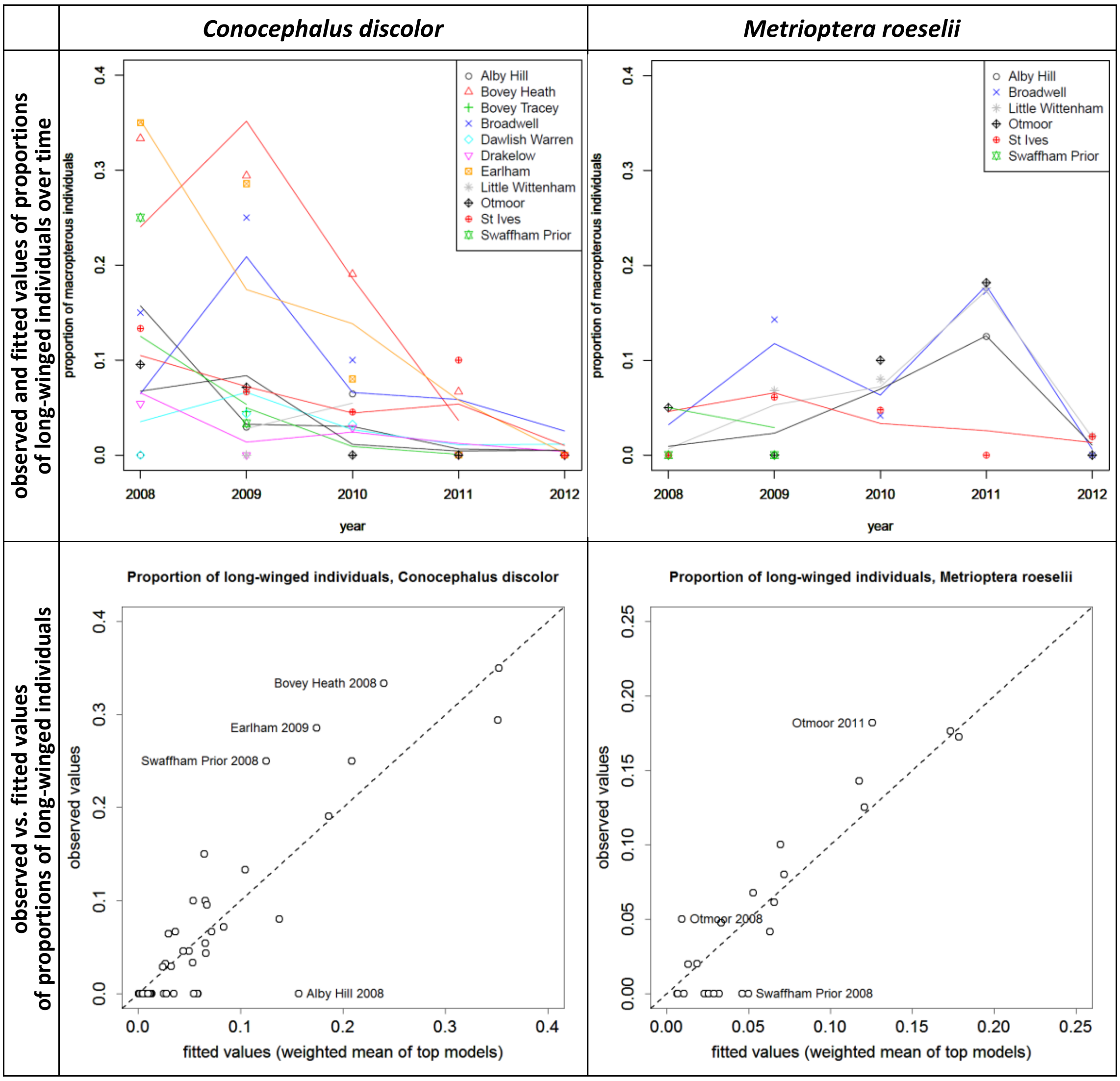


Fig 4.6. Observed and modelled values of proportions of long-winged individuals.

Top: Plots of observed and fitted values of proportions of long-winged individuals over time. Symbols indicate observed values of the proportions of long-winged individuals; lines in the corresponding colours indicate the weighted mean fitted values of top models (with ΔAIC < 4).

Bottom: Observed vs. fitted values of proportions of long-winged individuals. Fitted values are weighted means across sets of top models with ΔAIC < 4. Dashed lines indicate equality of observed and fitted values. Years and sites with the largest residuals are labelled. Note different scale of axes for plot for *M. roeselii* to other plots.

4.4.2.3 Correlations between predictors

Modelled correlations between fixed effects in sets of top GLMMs did not indicate any problematic collinearity between predictive variables for *C. discolor*, with all except two absolute values below 0.7. The exceptions were correlations between August to October rainfall of the study year and warmth of the same period (mean correlation value 0.73 ± 0.06), and warmth in the preceding year (correlation value -0.84); however, these variables only occurred together in very few of the 52 top models (4 and 1 respectively) (S 4.4a Table).

For *M. roeselii*, there were correlation values greater than 0.7 between several predictive variables, with one of these pairs of variables occurring in a large number of top models: April to July warmth and rainfall of the study year (mean correlation value 0.73, occurring in 106 of 148 top models) (S 4.4b Table).

4.5 Discussion

I present evidence for influences of seasonal weather on the range expansion process of two insect species in Britain, which have been expanding their distributions rapidly over the past 30-40 years. Colonisation rates inferred from long-term distribution monitoring data were significantly influenced by weather during times of year when juvenile development, and adult dispersal and reproduction, were taking place. There was some evidence for one study species in field surveys in 2008-12 for similar effects of seasonal weather on the incidence of long-winged (macropterous) individuals in sites near the range margins – likely to be the main mechanism for long-distance dispersal (Simmons and Thomas 2004). In the following, the strength of evidence for these findings is discussed, and the observed weather effects and their implications are reflected upon.

4.5.1 Strength of evidence

4.5.1.1 Distribution data and calculation of colonisation rates

The Grasshoppers and Related Insects Recording Scheme whose data was used here in the analysis of annual colonisation rates gathers records mostly without a standard protocol, and recording effort varies greatly over time and space; inferences therefore have to be drawn with caution (Isaac et al. 2014). The present analysis endeavoured to minimise bias due to these variations by calculating annual colonisation rate as the proportion of surveyed squares that were colonised within a typical maximum dispersal distance around the previously known distribution. Colonisation rate was therefore defined as the number of new squares recorded for the focal species relative to the number of squares recorded for all Orthoptera in the relevant year and geographical area. Potential bias due to a generally higher recording effort in warmer years, for example, or a generally higher detectability of insects like Orthoptera in warmer years due to higher activity (Ingrisch and Köhler 1998) should therefore be minimised.

Overall recording intensity for Orthoptera in Britain is intermediate compared to other recording schemes (Isaac et al. 2014). To aggregate records, therefore, data were analysed at a 10km square (hectad) level. The range expansions analysed here have proceeded through the south and east of Britain, i.e. the areas with the highest recording effort for this group, and the study period encompasses several semi-systematic surveys aiming at complete spatial and taxonomic coverage for two national and multiple county atlases (Marshall and Haes 1988, Haes and Harding 1997, Beckmann and Sutton 2013). Therefore, while recorded hectad colonisations may not always be records of the first individuals arriving in a square, their overall numbers are likely to reflect the temporal pattern of dispersal and establishment of new colonies. Both dispersal to new localities and the successful establishment and growth of populations there from initially low numbers (including arrival of additional colonists, see below) are necessary conditions for successful range expansions (Lockwood et al. 2013), and both of these processes may have influenced the pattern of recorded colonisation rates.

4.5.1.2 Models and modelling approach

Model fits were assessed by calculating the ratio of residual deviance to residual degrees of freedom. This should ideally be 1 (Crawley 2007), and the values observed here, of between 1.94 and 3.94 (S 4.6 Table), indicate a moderate degree of overdispersion (unexplained variation in the response variable). A way of compensating for this formally would be to use a quasi-binomial (rather than binomial) error structure. Using quasi-binomial errors does not change the estimated coefficients, but leads to an increase in standard errors and therefore potentially affects significance. With the moderate overdispersion of the binomial models used here, standard errors will not have been underestimated to a degree sufficient to alter conclusions; however, little emphasis should be placed on marginally significant results during interpretation of findings.

Sensitivity analysis of the colonisation rate models showed that, with one exception (August to October rainfall in the year of colonisation for *M. roeselii*), results were robust to a reduction in the assumed maximum typical dispersal distance for each species; to a change in the time period analysed, excluding all years without colonisations; and to a change in the definition of colonisation, including an assumption of extinction and re-colonisation of squares.

An issue that can arise with time series analysis is that subsequent data points may not be independent of each other, leading to temporal autocorrelation, for example due to population abundances in one year being partially dependent on abundances in the previous year (Chatfield 2003). Statistical methods such as Generalised Least Squares (GLS) can be used to account for such autocorrelation. An advantage of the binomial GLMs employed here over GLS is that estimates are constrained between 0 and 1 (appropriate for proportions), whereas least squares estimates (which assume normality) could potentially go beyond these boundaries. In the colonisation rate analysis (spanning 36 years), little correlation between the residuals of years *t* and *t+1* was found (Pearson's correlation coefficients of -0.07 for *C. discolor* and -0.14 for *M. roeselii* in the respective best models, and similarly low values across all top models). Equally, Durbin-Watson tests for autocorrelation between disturbances in time series, calculated assuming a linear relationship between year and colonisation rate, produced non-significant results for both species (DW = 1.8, p = 0.24 for *C. discolor* and DW = 1.8, p = 0.25 for *M. roeselii*) (Zeileis and Hothorn 2002). For the present study, therefore, temporal autocorrelation was not taken into account.

Time series may be "detrended" for analysis in order to remove spurious correlations arising from unrelated long-term trends in both predictor and response, for example by fitting a linear model of time vs. the data, and subtracting the fitted values from the original data (Crawley 2007). The inclusion of calendar year as a variable in the colonisation rate analysis here should go some way towards detrending the time series and avoiding undue influence of such correlations (see section 4.5.5 below).

Model selection needs to strike a balance between overfitting, i.e. selecting models with many covariates, which fit the data well but have little explanatory power (high variance), and underfitting, i.e. selecting overly simplistic models which may appear to have good precision (low variance), but may not fit the data well and may be biased because they omit important effects (Burnham and Anderson 2002). Here, the Akaike Information Criterion was used to select models, which is designed to facilitate finding this balance. AIC is defined as:

$$AIC = -2*\ln(\text{maximum likelihood}) + 2*p$$

where p is the number of parameters in the model (including the intercept). Lower AIC values indicate relatively better models, and AIC therefore penalises the inclusion of parameters which do not markedly improve overall model fit (Chatfield 2003, Crawley 2007). Other model selection procedures include stepping-up and stepping-down approaches, where parameters are added or taken out one by one, and pairwise comparisons of models are carried out at each step to assess whether deviance has changed significantly (Crawley 2007). These approaches may be very useful in identifying simple minimal adequate models. However, a disadvantage is that only nested models can be compared at each step, i.e. the parameters in one model must be a subset of those in the other, whereas model selection by

AIC allows comparison across all models, whether nested or not. In addition, stepwise model selection may rely on large numbers of pairwise tests, increasing the risk of detecting chance significant differences (multiple testing problem) (Burnham and Anderson 2002).

The multi-model inference approach employed here has the advantage of taking into account effects of sets of multiple top models with similarly good fits to the data (Burnham and Anderson 2002). However, despite the use of AIC for model selection, median numbers of variables in the sets of top models are relatively high in the colonisation rate analysis (8 for *C. discolor*, 9 for *M. roeselii*), given the sample size of 36 years. For the analysis of long-wingedness, where sample size for *C. discolor* was 46 and for *M. roeselii* 23, the number of variables per model was limited to a maximum of 6 from the outset, because more variables led to some model convergence failures (cf. section 4.3.2.3). Numbers of parameters per model would potentially be reduced more generally for both analyses by using a corrected AIC (AICc) which penalises inclusion of additional model parameters more than the uncorrected AIC in cases where the ratio of sample size to number of explanatory variables is small (Burnham and Anderson 2002). Use of AICc here would therefore also be likely to reduce the numbers of top models across which results are averaged. These could be reduced further by decreasing the upper limit of AIC values to include (for example by including models only up to ΔAIC=2). However, the use of Akaike weights in the model averaging process employed here means that models with greater AICs have a limited influence on overall results in any case (cf. section 4.3.1.4).

4.5.1.3 Analysis of macroptery and field survey data

For the analysis of seasonal weather effects on macroptery, three parameters describing conditions during field visits were included in order to account for potential biases: day of year, time of day, and mean temperature on the day. For *C. discolor*, none of these had significant effects, indicating that recording of long-winged individuals was not biased due to the particular conditions of field visits. For *M. roeselii*, there were near-significant ($p<0.1$) effects of time of day and temperature, indicating potential effects of these parameters on proportions of macropters observed; this may be due to the low sample size for this species. There were larger sets of top models with equivalent explanatory power in the analysis of weather effects on macroptery than in the analysis of colonisation rates, particularly for *M.*

roeselii (148 models), most likely also reflecting the modest sample sizes for the estimation of macroptery proportions.

For *C. discolor*, there was some evidence for similar seasonal weather conditions affecting the incidence of dispersive macropters as affected colonisation rates. Since macropters are likely to be the main mechanism for long-distance dispersal, the findings from these two different datasets corroborate each other (Simmons and Thomas 2004). However, the strength of evidence for these agreements was limited: one agreement between significant effects, and three agreements between significant and near-significant effects, albeit with no evidence for an interaction between the effects of April to July warmth and rainfall on macropterism. It may be that the observed near-significant weather effects on macropterism would have been significant with a larger sample size, and / or if the study had been carried out over more than five years, allowing more variation in weather to occur.

There was no agreement between weather effects on colonisation rates and macropterism for *M. roeselii*. This may again be due to the limited study period and the low overall sample size, and also the small number of newly colonised sites surveyed for this species (only one site at the current range margin was surveyed in more than one year). Presumably also partly due to the low sample size were correlations between several predictive variables, particularly between April to July warmth and rainfall of the study year, which were not evident for *C. discolor* (S 4.4a+b Tables). Overall, the findings for weather effects on incidence of macropterism in *M. roeselii* are considered insufficiently reliable to draw conclusions from.

4.5.2 Interacting positive effects of warm and wet April-July periods

For both study species there was evidence that warm and wet conditions during the period of hatching and juvenile development (April to July) significantly increased colonisation rates, with a significant positive interaction between these effects in 100% of top models. This suggests that high sums of warmth were especially positively related to colonisation rates in wet years.

A positive effect of spring and early summer warmth on dispersal and colonisation rates agrees with my hypotheses. Warm weather during juvenile development has been found to lead to higher abundances in many insects, presumed due to increased growth rates and reduced mortality (Ingrisch and Köhler 1998, Roy et al. 2001, Poniatowski and Fartmann 2011c). In turn, higher densities are likely to increase emigration (Travis and Dytham 2012) and, in the study species here, numbers of individuals developing into dispersive long-winged macropters (Ingrisch and Köhler 1998, Poniatowski and Fartmann 2011c).

A positive effect of wetter conditions during April to July on colonisation rates and numbers of macropters, however, is partly contrary to my hypotheses. I had expected low, or intermediate, rainfall during juvenile development to have the greatest positive effect, since wet conditions lead to colder microclimates and slower growth rates (Ingrisch and Köhler 1998) and I therefore expected, to lower densities and dispersal, while I expected desiccation only to be a problem in extreme cases (Ingrisch 1984, Oliver et al. 2015b). However, the results here suggest that high rainfall had a positive effect (and / or low rainfall a negative effect) in years of average or above-average warmth during the same months.

The significant interaction between the effects of rainfall and warmth on range expansion is a novel finding to my knowledge, and may go some way to resolving apparent contradictions between previous studies, some of which found a negative effect of rainfall on development of macropters (Poniatowski and Fartmann 2011c), while others suggested positive effects (Ingrisch and Köhler 1998). Some previous studies have shown abundances of insect species of moist or semi-shaded habitats to increase with high rainfall (Roy et al. 2001) and densities to be higher in moister habitats (Poniatowski and Fartmann 2011a) (for *M. roeselii*), while abundances decreased in exceptionally hot and dry conditions (Oliver et al. 2015b). Both study species here favour tall herbaceous vegetation; high moisture is therefore likely to produce suitable vegetation structures, and may also improve food plant quality. Interestingly, however, the present results suggest that species can take advantage of these only if there is sufficient warmth at the same time. This may therefore be a parallel at shorter temporal scales to indications that recent climatic warming is creating suitable microclimates for several insect species in taller vegetation than they previously utilised (Thomas et al. 2001, Pateman et al. 2012, Beckmann et al. 2015, Pateman et al. 2016).

The findings of the present study suggest that where possible effects of warmth and moisture should not be looked at in isolation. The reason that this study is the first to observe interacting effects of these parameters on range expansion may be that they tend to be (negatively) correlated and are therefore difficult to investigate together (Poniatowski and Fartmann 2011c). It may be that correlation was reduced here through a long study period of 36 years and through considering weather effects summed over several months rather than for individual months. Similar designs may therefore enable future studies to include interactions of warmth and moisture.

For *C. discolor* there was also a positive effect of April-July rainfall of the previous year on incidence of macropterism (and a near-significant effect on colonisation rate). This may be due to favourable conditions leading to a build-up of numbers in the parental generation, resulting in higher starting densities in the subsequent year (Poniatowski and Fartmann 2011c).

4.5.3 Positive effects of warm (and dry) August-October periods

In agreement with my hypotheses I found evidence for positive effects of warm weather during August to October on colonisation rates in both study species (and a near-significant effect on numbers of long-winged individuals in *C. discolor*). For *C. discolor*, there was also a significant positive effect of low rainfall during August to October of the previous year on both colonisation rates and numbers of macropters. The conditions triggering insect dispersal events are not yet fully understood (Clobert et al. 2012), but insect flight activity generally is known to be strongly influenced by temperatures (Pollard 1977, Uvarov 1977), potentially increasing dispersal distances (Walters et al. 2006). Anecdotal evidence suggests that dispersal flights of macropterous bush-crickets occur on warm, dry and still days (Smith 2007, Rudkin 2012).

By creating warmer microclimates, dry conditions during August to October in the preceding year may also entail higher metabolic rates and reproductive output, leading to higher densities and greater dispersal in subsequent years (Ingrisch and Köhler 1998, Poniatowski and Fartmann 2011c). The fact that the present study found a positive effect of moisture during April-July (if coupled with warmth), but a negative or no effect of moisture during August-October may support the conclusion that the main benefit of increased moisture to the study species is through increased vegetation height and food plant quality during juvenile development: most plant growth happens during the earlier part of the season, with rainfall during April-July likely to affect vegetation structure more than during August-October (Parton et al. 2012). Dry weather in August-October is therefore likely to mean warmer microclimates with little adverse effects on vegetation structure.

As indicated above, an apparent positive association of August to October rainfall with colonisation rates of *M. roeselii* was not robust to a change in the start year of the analysis or a changed definition of colonisations and is therefore not considered reliable.

4.5.4 Waves of range expansion in favourable years

Seasonal weather-dependence of the colonisation process as observed in the present study is likely to lead to stochastic colonisation patterns, and to range expansions proceeding in waves rather than at a steady rate (cf. Fig 4.5 top), with 0% up to 40% (in *C. discolor*) or 45% (in *M. roeselii*) of target hectads being colonised in different years. These patterns are likely to be amplified by the interaction of effects observed between warmth and rainfall. Taking species' sensitivity to variations in seasonal weather into account, rather than basing studies on averaged trends (in climate and distribution) should improve models for past climate-driven range changes and increase the predictive power of model projections into the future (Henry et al. 2014).

Many insects can respond rapidly to favourable environmental conditions due to their short generations and large numbers of potential offspring. High phenotypic plasticity in dispersal, as in wing-dimorphic species, may be an additional adaptation to variable environments (Pigliucci 2005), allowing species to rapidly take advantage of temporary resources (Uvarov 1966). Even under sustained changes in mean environmental conditions, such as current climatic warming, a stochastic dispersal pattern may provide selective advantages: focusing dispersal events into waves is likely to increase the chances of individuals finding conspecific mates at new sites, decreasing the likelihood of local founder effects occurring (Hochkirch and Damerau 2009) and counteracting Allee effects (Kindvall et al. 1998, Travis and Dytham 2002, Kaňuch et al. 2014). Density dependence may also be contributing to the benefits of periodic dispersal (see below).

High phenotypic plasticity of dispersal may also be a selective advantage in fragmented landscapes, allowing species to persist in suitable habitat patches (with brachypters which have higher fecundity investing in local reproduction) and invest in dispersal and colonisation of new sites only sporadically and under favourable conditions. However, if fragmentation is so severe – or habitat requirements of species are so specific – that colonisation attempts generally fail, stochastic dispersal of large proportions of individuals may increase the likelihood of local extinctions. The two present study species are fairly generalist in their habitat requirements (Beckmann et al. 2015) and this combination of traits is evidently allowing them to expand across fragmented landscapes and consolidate distributional gains successfully.

April to October temperatures in Britain have increased significantly over the study period, and are projected to continue rising throughout this century, while rainfall has increased slightly or stayed level and is projected to remain so or decline slightly (UK Met Office 2012, Thackeray et al. 2016). I therefore expect weather conditions to remain suitable for further range expansion of the study species.

4.5.5 Increase in colonisation rate over time for *M. roeselii*

For *M. roeselii*, there was a significant overall increase in colonisation rate over time, over and above the effects of weather (and the non-significant trend (present in 44% of best models) for *C. discolor* was in the same direction) (Table 4.1, Fig 4.5). This suggests that for *M. roeselii* there were factors in addition to the weather parameters included in the current study which affected colonisation rate over time. One such factor is likely to be evolutionary development towards increased dispersal in the course of the range expansion process, which previous studies suggest has taken place in both species – both a lowering of the density threshold triggering development of macropters, and an increase in the flight ability of macropters (Simmons and Thomas 2004, Travis et al. 2009) (see below). My findings here may indicate that this evolution has been more pronounced in *M. roeselii* than in *C. discolor*, or may be due to variation in the statistical detectability of a trend between the two species through other factors.

4.5.6 Population density and macropterism

In my field surveys I found a significant negative association of population density with proportions of long-winged individuals for *C. discolor*, and no association for *M. roeselii* (Table 4.1). Previous studies have produced varying results: while (Simmons and Thomas 2004) found negative density dependence of macropterism for *C. discolor* in both field and laboratory observations, and mixed results for *M. roeselii* (negative density dependence in field observations at range margin sites only, and contrasting positive / negative density dependence across all sites depending on the measure of density used), the majority of studies have found positive density dependence of macropterism in these and other Orthopteran species (Ando and Hartley 1982, Ingrisch and Köhler 1998, Behrens and Fartmann 2004, Poniatowski and Fartmann 2011c).

These differences are likely to be due in part to temporary evolution of dispersal during range expansions, and therefore to depend on whether expanding or static, and range core or range margin populations are sampled (Simmons and Thomas 2004, Travis et al. 2009). Assuming that development of macropters in range core populations is triggered by high densities, as most studies suggest, the threshold of response may be lowered temporarily by evolution at the advancing range margin during sustained range expansions. If marginal populations (initially at low density) did not produce macropters until high densities were achieved (potentially many years later), range expansion would be expected to be slow. The expanding 'front' of range expansion is likely to be formed of successive generations of individuals with low thresholds to develop into macropters. These will colonise new sites and mate with each other in a positive feedback loop. Near the range margin, development of macropters is therefore expected at significantly lower densities than in the range core (Travis et al. 2009), explaining why, in the previous study of *C. discolor* and *M. roeselii* in Britain, range margin populations produced larger numbers of long-winged individuals when reared in the lab and controlling for density (Simmons and Thomas 2004). Over time, the threshold is then likely to increase again because of a trade-off between energetic expenditure on dispersal and on other traits including egg and spermatophore production, with selection favouring greater numbers of brachypters again once the expanding range margin has moved on (Emlen 2001, Simmons and Thomas 2004, Burton et al. 2010).

While a reversal of density-dependence (from positive to negative) could potentially evolve, this cannot be deduced from my field data. The negative association between density and macropterism in my data may be due to the correlation between a lower threshold of response (with density-dependence remaining positive) at recently colonised range margin sites and lower densities at the same sites (although there was no significant association between density and distance from core or age of population in the present study for *C. discolor* (but for *M. roeselii* older populations did tend to have higher densities) (S 4.10 Table)). Furthermore, some of the macropters observed may have already dispersed at the start of their adult lives (potentially from higher-density populations), rather than originating at the sites where they were sampled (Poniatowski and Fartmann 2011c). This pattern might be reinforced behaviourally if dispersing macropters tend to settle in low- or medium-density populations in preference to high-density sites (Hochkirch and Damerau 2009, Travis and Dytham 2012). Further investigations are needed to resolve these questions more fully, ideally tracking origins and dispersal movements of macropters in relation to population densities.

I did not find a significant effect of the distance from the population core on numbers of macropters, unlike (Simmons and Thomas 2004). This is not surprising given that, in contrast to the earlier study, all my field sites were selected to be near the current or recent range margins. Also, unlike the earlier study, my sites were sampled over a period of 5 years, allowing more variation in weather to occur, while the distance to the range core remained constant, explaining why I detected some effects of weather and the earlier study did not.

4.5.7 Dispersal distances

The “typical maximum dispersal distances” of 31.6 km for *C. discolor* and 28.8 km for *M. roeselii* calculated in the present study are very large compared to studies based on direct observations such as mark-release-recapture (Ingrisch and Köhler 1998). However, other methods have inferred larger dispersal distances, for example genetic tests of macropterous individuals of *M. roeselii* during a favourable (hot) year indicated mean dispersal distances of 8 km and a maximum of 19.1 km (Hochkirch and Damerau 2009). Similarly, a regional analysis of 1-2km grid square distribution records during range expansion in north-western Germany found maximum dispersal distances for *M. roeselii* of 5.1-6.3 km (Wissmann et al. 2009). In flight tunnel experiments, macropters of *C. discolor* flew a mean of 12.3 km to exhaustion in a single sitting, i.e. without major breaks for resting or feeding, with individuals from the expanding range margin flying a mean of 16.7 km (Simmons and Thomas 2004). The maximum typical dispersal distances calculated in the present study therefore seem plausible. I observed a small number of annual dispersal distances in excess of these figures – up to a maximum of 216 km for *C. discolor* and 166 km for *M. roeselii* (cf. Fig 4.3). Some of these may reflect anthropogenic dispersal (Kaňuch et al. 2013), although wind-assisted flight cannot be entirely excluded as a possibility.

4.6 Conclusion

This study investigated effects of annual variations in seasonal weather on the rapid range expansion over the past four decades of two temperate insects at their north-western range margins in Britain, *Conocephalus discolor* and *Metrioptera roeselii* (Orthoptera: Tettigoniidae). I hypothesised that both seasonal temperature and rainfall would influence the range expansion process here. Both species are wing-dimorphic, with a distinct long-winged (macropterous) dispersal morph, which is likely to be responsible for much, if not all, of the long-distance dispersal. The distributions of both species have been monitored by the Grasshopper Recording Scheme since 1968, allowing me to investigate effects of seasonal weather in two different and complementary ways: an analysis of annual colonisation rates from long-term distribution data, and an analysis of numbers of macropters found near the current or recent range margins, based on field surveys.

I found evidence for significant effects of April to July weather on colonisation rates in both study species, with a combination of warm and wet conditions increasing colonisation rates. There was a positive interaction between temperature and rainfall, such that colonisation rates increased for both study species when both warmth and rainfall were high, contrasting with little or no increase if either weather parameter was low. I attribute these findings to the interacting effects of warmth and moisture on microclimates and vegetation structure during the period of juvenile development, although the precise mechanisms still need to be established. Warm microclimates increase development rates, potentially leading to reduced mortality, higher population densities and increased emigration. Wet conditions reduce the risk of desiccation of sensitive insect stages, and boost plant growth, increasing food and habitat quality for the study species, both of which favour tall herbaceous vegetation. However, wetter weather and taller vegetation also mean cooler microclimates, so it is interesting that there was a positive effect of increased rainfall particularly during warm years. To my knowledge my study is the first to observe such an interacting effect of temperature and moisture on range expansion; the finding suggests that where possible these parameters should not be looked at in isolation, as wrong conclusions may be drawn. For example, low rainfall may have a neutral or even positive effect in a cold year, but a negative effect in a warm year, or levels of range expansion may be underestimated by extrapolating temperature effects on colonisation observed during a dry period.

There was also evidence for positive effects of warm weather during August to October on colonisation rates for both study species. For *C. discolor* there was also a significant effect of low rainfall in August to October of the preceding year on both colonisation rate and macroptery. Warm (and / or dry) conditions create warmer microclimates and increase insect activity levels and dispersal distances. Increased metabolic rates under warm microclimates may also raise reproductive output, leading to higher densities in subsequent years, and facilitating establishment of new populations from initially low numbers.

The results suggest that annual variability in seasonal weather may significantly influence expansion rates, and future range changes of sensitive species are likely to proceed at variable speeds, with waves of increased expansion in, or following, favourable years. A stochastic dispersal pattern might provide selective advantages by concentrating dispersal events, with potential benefits for establishment through greater numbers of colonists arriving at the same time. Waves of dispersal might also be a selective advantage in fragmented landscapes, allowing species to persist in suitable habitat patches and invest in dispersal only sporadically and under favourable conditions.

The stochasticity of seasonal weather means that an element of unpredictability to future range expansions of sensitive species will remain, but incorporating information about this sensitivity should improve model fits to past expansions and increase accuracy of model projections into the future. Given the scale of projected changes in climate over this century, a detailed understanding of likely effects on species will be critical for planning conservation responses and developing management strategies.

5. Informing a standardised method for Orthoptera abundance and site monitoring

5.1 Abstract

With rapid climatic and land use changes affecting many habitats and species, there is an urgent need to monitor species' populations in order to understand how these changes are affecting them, to enable conservation decisions to be based on good evidence. Britain is fortunate in having a strong tradition of biological recording by volunteers, and for many species groups distributions are being successfully monitored through unstructured recording. Systematic monitoring of abundances is much rarer, particularly for invertebrates. Rigorous abundance monitoring protocols can put recorders off, and survey designs need to strike a balance between the quality and quantity of data collected. Where abundance monitoring data is successfully collected, it has proved invaluable in assessing the conservation status of species, identifying drivers of decline, and investigating wider biological and ecological questions. This chapter aims to develop a preliminary protocol for Orthoptera abundance monitoring that is suitable for volunteer participation, and presents a power analysis in order to estimate what degree of population change might be detectable for different species using this approach.

It is proposed to carry out a combination of acoustic transect counts, box quadrats and beating, along existing transect routes used for butterfly and bird monitoring: counting the number of stridulating males of each species heard with a bat detector along the transect; placing a 1x1m, 75cm high box quadrat at the start and mid-point of each transect section and searching it for 1 minute; and beating the nearest trees or bushes for 1 minute after each quadrat count using a 100x75cm beating tray (folded box quadrat). Three counts per year are proposed during the time of peak adult abundance of most Orthopteran species: July, August and September, with surveys conducted during the time of highest acoustic activity for the majority of species: between 9:00 and 18:00. The weather should be as warm, sunny and still as possible, with a minimum temperature of 18°C and a maximum wind speed of 3 Beaufort (19km/h). Counts carried out in this way should provide abundance measures for most species in Britain.

Results of a power analysis parameterised from existing literature and trial acoustic transect counts carried out in 2016 suggest that for abundant species on good quality habitat (with an assumed starting count of 60 individuals), between 24 and 52 sites would be needed to detect a 30% decline over ten years, depending on the variability of populations and sampling accuracy. For rare species on good quality sites, or species on poor quality habitat (with an assumed starting count of 6 individuals), slightly higher numbers of between 30 and 80 sites would be needed to detect such a 30% decline. Considerably higher numbers of sites would be required to reliably detect smaller declines of 15% over ten years: between 90 and 244 sites for abundant species on good quality habitat, and between 126 and 364 sites for rare species or poor quality habitats, depending on the variability of populations and sampling accuracy.

Thorough field trials of the proposed method will be required in order to evaluate sampling variability and accuracy, and to assess whether recorders find the method practicable and enjoyable, and if there are aspects which need revision. The numbers of recorders an Orthoptera abundance monitoring scheme is able to attract and retain, and therefore the types of species and magnitudes of declines it can expect to monitor successfully, will depend on factors including how enjoyable or onerous the protocol is perceived to be, and how much organisational support is provided, including feedback and training for recorders. If a future Orthoptera abundance monitoring scheme manages to strike a successful balance between encouraging wide participation and collecting accurate data, it can greatly support the study and effective conservation of an important and popular group of insects.

5.2 Introduction

5.2.1 The need for monitoring

Loss of biodiversity is proceeding at rapid rates across many regions, habitats and species groups, raising concerns for the conservation of many species, and the resilience of ecosystem services and natural capital (Millennium Ecosystem Assessment 2005a, Oliver et al. 2015a, Hayhow et al. 2016). There is therefore an urgent need to monitor populations in order to set and report against conservation targets, aimed at slowing or reversing declines. Population monitoring data are essential for assessing impacts of environmental change as well as the efficacy of conservation measures, so that resources available for conservation can be spent effectively (Sutherland et al. 2004). Particularly in economically difficult times environmental budgets such as agri-environment payments may come under pressure, and expenditure for conservation requires a strong evidence base in order to maintain its place on the political agenda.

5.2.2 Citizen science and current monitoring

Observing effects of environmental change on the natural world over large areas and long time periods requires collection of big amounts of data. Many surveys successfully enlist the help of volunteer recorders in order to achieve such large-scale and long-term coverage (Hochachka et al. 2012). Now often referred to as “citizen science”, this approach has proved very effective, contributing to the creation of many of the most important monitoring datasets. At the same time, it provides opportunities for scientists to disseminate findings to a wider audience, and for naturalists and others with a love of a particular species group or area to pursue their interest, develop their knowledge, and gain insights into the process of scientific investigation (Bonney et al. 2009, Miller-Rushing et al. 2012).

Methods of volunteer-based biological record collection range from opportunistic recording of species distributions to systematic, randomised monitoring of abundances (Isaac and Pocock 2015). Different methods produce different qualities of data, and are suited to recorders of different levels of expertise (Pescott et al. 2015). There is often an important trade-off between the quality and quantity of data collected, and citizen science projects need to strike a balance between scientific rigour and providing an enjoyable experience to participants, which will make broad and sustained participation more likely (Dickinson and Bonney 2012). Offering different “levels” within a survey can be a useful way to appeal to all recorders and simultaneously provide opportunities to learn and progress (Pescott et al. 2015).

Britain has a particularly strong tradition of biological recording going back to the Victorian collectors of the 19th century and beyond, and many species groups have long-standing dedicated recording schemes (Pocock et al. 2015b). Most of these carry out opportunistic distribution recording, with periodic atlas publications providing an incentive for semi-structured targeting of recording effort to maximise coverage. With the exception of birds, butterflies, moths and aphids, and more recently bats, herptiles, plants and pollinators, there is very little systematic monitoring of abundances, particularly for invertebrates. For

Orthoptera, a national recording scheme has collected opportunistic distribution records since 1968 (chapter 2). There is currently no structured survey of Orthoptera abundances in Britain, and no consensus on the most suitable standard methods (Gardiner et al. 2005).

5.2.3 Uses and limitations of opportunistic distribution monitoring

Opportunistic distribution monitoring has proved invaluable in establishing the basic distributions of many species, and changes therein at broad spatial and temporal scales (Preston 2013). Recent developments in statistical methods have increased the power and robustness of detecting trends from such unstructured distribution recording data: annual estimates of occupancy which are robust to several biases and have good statistical power to detect trends can now be derived for species with medium to large amounts of data (currently thousands of records per species) (van Strien et al. 2013, Isaac et al. 2014, Fox et al. 2015, Hayhow et al. 2016).

However, several limitations of opportunistic distribution recording for trend estimation remain. Firstly, recording is frequently biased in its coverage, for example with higher numbers of records in or near urban areas, or at high quality sites such as nature reserves which are more interesting for recorders to visit, affecting the representativeness of the occupancy estimates (Pescott et al. 2015). Secondly, being based on “presence-only” data, species absences have to be inferred from lists of other species recorded, relying on a number of assumptions about recorder behaviour (chapter 2). Thirdly, trend analysis generally requires a large amount of data (although work is ongoing to reduce the minimum number of records needed (Eaton et al. 2015)) – and inferences are therefore not possible / reliable for rarer species (Bried and Pellet 2012), and for other species may have to be made at very large (national) scales and across all habitats, i.e. may not allow assessment of specific habitats or sites. Finally, occupancy model analyses are typically restricted to “high quality” data, which are precisely specified in time and space, and have a minimum of two (or more) species recorded during a visit (Isaac et al. 2014, August et al. 2015b); this means that the majority of opportunistic records is often discarded during analysis – which is not an efficient use of recording efforts.

5.2.4 Advantages of structured abundance monitoring

While structured abundance monitoring has the disadvantage of being more prescriptive and labour-intensive than opportunistic distribution recording, and therefore may attract fewer volunteer recorders, it offers a number of advantages if carried out successfully and achieves sufficient participation.

Firstly, if monitoring sites are selected in a random (or stratified-random) manner, assessments are representative, allowing species' conservation statuses to be assessed more robustly. Randomised surveying should also allow detection of population trends in widespread species not apparent from monitoring of semi-natural, high-quality, protected habitats alone (Cowley et al. 1999, Roy et al. 2005, Roy et al. 2007).

Secondly, standardised abundance monitoring allows the assessment of population trends at specific sites, beyond merely recording presence or absence. For example, the UK Butterfly Monitoring Scheme's primary sampling method of transect walks has become an important tool for site monitoring and conservation of butterflies (Pollard and Yates 1993, Thomas 2005, van Swaay et al. 2008). Population trends can also be compared between sites, for example to assess effects of conservation interventions, with a potential to use sites where no management was applied as controls (Sutherland et al. 2004). An important caveat is that detectability of species may vary between sites (for example due to differences in habitat) and abundance estimates for any one year may not be comparable between sites (unless detectability is measured) (Pellet et al. 2012). However, *trends* in abundance estimates can be compared between sites, provided that detectability does not change over time.

Thirdly, declines in species can be difficult to detect from distribution data alone, particularly for widespread species and when data are summarised at coarse spatial scales such as for national maps (chapter 2), because many local populations may need to go extinct before a grid square is lost (Thomas and Abery 1995). Abundance monitoring may allow detection of ongoing declines sooner, and may therefore also facilitate identification of the causes of declines, and implementation of appropriate conservation actions (Thomas et al. 2006).

Fourthly, collection of abundance data allows investigation of a wider range of ecological and biological questions than distribution data alone, such as long-term population dynamics; the interplay between population density and range expansion (chapter 4); population effects of natural enemies, and conversely, importance of species in the food web; and relative changes of abundances in different habitats, or different latitudes within a species' range (Cowley et al. 2001a, Cowley et al. 2001b, Hill et al. 2011, Oliver et al. 2012).

Finally, advances in modelling now allow combining systematic abundance recording data and opportunistic distribution data in hierarchical models. In other words, it is not a choice between one or the other method and the strengths of both can be combined, yielding improved estimates of changes in populations across space and time (Pagel et al. 2014).

5.2.5 Why monitor Orthoptera?

Insects have been found to react more rapidly to environmental changes than other species groups such as birds and plants, meaning they can provide important early warning signals (Thomas et al. 2004b). Currently there are very few large-scale abundance monitoring datasets for invertebrates other than Lepidoptera, and while there are reasons to believe that butterflies are representative of other insects there is still an urgent need to monitor additional invertebrate groups (Thomas and Clarke 2004, Thomas 2005).

As ectothermic species of mostly open habitats, Orthoptera are very sensitive to changes in environmental conditions, and populations respond rapidly to climatic and land use changes, making them excellent indicators (Benton 2012, Beckmann et al. 2015). In Europe, Orthoptera are the most threatened taxonomic group for which assessments have been carried out, with over 25% of species threatened with extinction (Hochkirch et al. 2016). Their primary habitats, semi-natural grasslands, face multiple pressures from intensification of use and nutrient enrichment to abandonment, with the European Grassland Butterfly Indicator showing a 30% decline in abundances between 1990 and 2013 (van Swaay et al. 2015). There is a strong need for monitoring of Orthopteran populations and further development of conservation measures for their habitats.

As large and abundant insects Orthoptera can form a large proportion of insect biomass, providing food sources for threatened or declining birds and other species such as reptiles, small mammals and spiders (Ingrisch and Köhler 1998, Benton 2012). While none of the Orthopteran species in Britain are currently of economic significance, they are important both as human food source and as agricultural pests in other parts of the world (van Huis et al. 2013).

Grasshoppers and crickets are popular insects due to their song and remarkable jumping ability. Learning to identify the currently 30 species established in the wild in Britain is a manageable task, and importantly, all can be identified to species in the field, making the group very suitable for volunteer recording. The fact that the majority of Orthopteran species produce loud, species-specific songs is unique among insects in Britain, and offers great advantages for recording: songs make species detectable and identifiable across many different habitats and at distances of several meters, and counts of singing males have been shown to be an effective method for monitoring densities (Fischer et al. 1997, Ragge and Reynolds 1998).

There is currently no structured survey of Orthoptera abundances in Britain, and no standard method. “There is an urgent need for development of a standardised sampling technique that can produce comparable data from studies with a wide variety of observers in grasslands with differing vegetation structures and grasshopper densities” (Gardiner et al. 2005).

5.2.6 Aims & approach of present study

The aim of this chapter is to develop a preliminary protocol for Orthoptera abundance monitoring in Britain suitable for use by volunteers. It is informed by a review of relevant literature, analysis of existing data, and a first trial of methods in 2016. In addition, a power analysis is carried out using relevant parameters from the literature and the first trial of methods in 2016 in order to assess the potential of such a monitoring scheme to detect changes in abundances depending on the number of sites surveyed. A pilot study will be required to assess and test the proposed protocol fully with a range of volunteers before it could be rolled out.

5.3 Survey design

5.3.1 Number of visits

Experience from existing volunteer-based monitoring schemes suggests that there is a trade-off between the amount of sampling effort required by a survey's methodology (and therefore the potential accuracy of sampling), and the likely number of participants (and therefore the potential number of sites surveyed) (Tweddle et al. 2012, Stanbury et al. 2015).

A study which sub-sampled data of the UK Butterfly Monitoring Scheme concluded that reducing numbers of annual visits and focusing on the time of peak abundance still produced good statistical power: a 3-visit scheme achieved equal power to the full 26-visit scheme with an average of only twice as many sites sampled, and a 2-visit scheme with three times as many sites sampled (Roy et al. 2007, Brereton et al. 2011). The latter was selected as the minimum required in the UK Wider Countryside Butterfly Survey (Brereton et al. 2011).

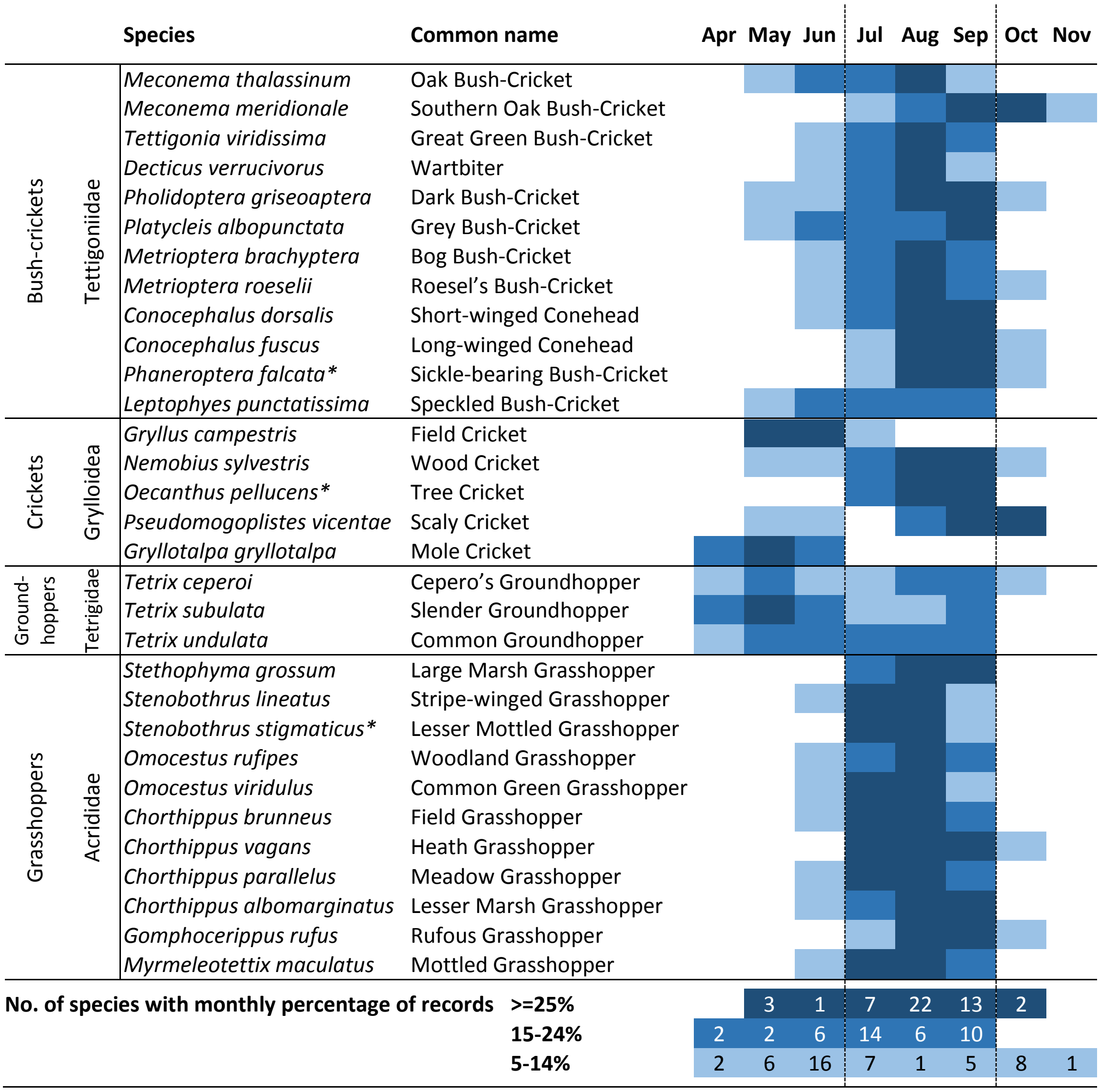
In order to maximise likely participation and provide good efficiency, a small number of visits during the time of peak abundance is proposed. For analysis purposes, it may be useful to survey a small number of sites more frequently in order to be able to detect and account for annual variations in emergence dates (Roy et al. 2007). Alternatively, for species with sufficient opportunistic distribution data these could be used to estimate phenology (Bishop et al. 2013).

5.3.2 Time of year

The season of peak abundance for most Orthoptera in Britain is July to September (Evans and Edmondson 2007, Benton 2012), reflected in monthly numbers of observations in the Orthoptera recording scheme database (Fig. 5.1). Bush-crickets (Tettigoniidae) and crickets (Grylloidea) tend to have peak numbers of observations during August and September, while grasshoppers (Acrididae) tend to have slightly earlier phenologies, with most records during July and August.

Two species with restricted distributions, Field and Mole crickets (*Gryllus campestris*, *Gryllotalpa gryllotalpa*) form an exception, with most records occurring around May; the very few sites where these species occur in Britain would require additional surveys earlier in the year to cover their periods of peak activity. The Scaly Cricket (*Pseudomogoplistes* *vicentae*) can be found all year round (Sutton 1999, Benton 2012); however, its specialised shingle habitat means that it is not suitable to be monitored as part of a survey for other Orthopteran species and would therefore require separate, targeted surveys.

The groundhoppers (Tetrigidae) have long seasons of activity, with a bimodal pattern of observation numbers in Britain (Fig. 5.2): an early peak from April to June during the main period of reproduction, followed by a dip as adults die off, and a second peak during August and September as the new generation emerges. Surveys during (July to) August and September would be suitable to cover the second peak of abundance, although individuals observed will be immature adults or nymphs (Benton 2012).



		Species	Common name	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Bush-crickets	Tettigoniidae	*Meconema thalassinum*	Oak Bush-Cricket		░	▨	▨	■	░		
		Meconema meridionale	Southern Oak Bush-Cricket				░	▨	■	■	░
		Tettigonia viridissima	Great Green Bush-Cricket			░	▨	■	▨		
		Decticus verrucivorus	Wartbiter			░	▨	■	░		
		Pholidoptera griseoaptera	Dark Bush-Cricket		░	░	▨	■	■	░	
		Platycleis albopunctata	Grey Bush-Cricket		░	▨	▨	▨	■		
		Metrioptera brachyptera	Bog Bush-Cricket			░	▨	■	▨		
		Metrioptera roeselii	Roesel's Bush-Cricket			░	▨	■	▨	░	
		Conocephalus dorsalis	Short-winged Conehead			░	▨	■	■		
		Conocephalus fuscus	Long-winged Conehead				░	■	■	░	
		*Phaneroptera falcata**	Sickle-bearing Bush-Cricket				░	■	■	░	
		Leptophyes punctatissima	Speckled Bush-Cricket		░	▨	▨	▨	▨		
Crickets	Grylloidea	*Gryllus campestris*	Field Cricket		■	■	░				
		Nemobius sylvestris	Wood Cricket		░	░	▨	■	■	░	
		*Oecanthus pellucens**	Tree Cricket				▨	■	■		
		Pseudomogoplistes vicentae	Scaly Cricket		░	░		▨	■	■	
		Gryllotalpa gryllotalpa	Mole Cricket	▨	■	▨					
Ground-hoppers	Tetrigidae	*Tetrix ceperoi*	Cepero's Groundhopper	░	▨	░	░	▨	▨	░	
		Tetrix subulata	Slender Groundhopper	▨	■	▨	░	░	▨		
		Tetrix undulata	Common Groundhopper	░	▨	▨	▨	▨	▨		
Grasshoppers	Acrididae	*Stethophyma grossum*	Large Marsh Grasshopper				▨	■	■		
		Stenobothrus lineatus	Stripe-winged Grasshopper			░	■	■	░		
		*Stenobothrus stigmaticus**	Lesser Mottled Grasshopper				■	■	░		
		Omocestus rufipes	Woodland Grasshopper			░	▨	■	▨		
		Omocestus viridulus	Common Green Grasshopper			░	■	■	░		
		Chorthippus brunneus	Field Grasshopper			░	■	■	▨		
		Chorthippus vagans	Heath Grasshopper				■	■	■	░	
		Chorthippus parallelus	Meadow Grasshopper			░	■	■	▨		
		Chorthippus albomarginatus	Lesser Marsh Grasshopper			░	▨	■	■		
		Gomphocerippus rufus	Rufous Grasshopper				░	■	■	░	
		Myrmeleotettix maculatus	Mottled Grasshopper			░	■	■	▨		
No. of species with monthly percentage of records			**>=25%**		3	1	7	22	13	2	
			15-24%	2	2	6	14	6	10		
			5-14%	2	6	16	7	1	5	8	1

Fig. 5.1: Phenology of Orthoptera in Britain.

Colours indicate the percentage of records for each species in the Orthoptera Recording Scheme database between 1980 and 2015 which fall within a month: dark blue ≥25%, medium blue 15-24%, light blue 5-14% (Orthoptera Recording Scheme 2015a, b). Dashed lines indicate the period July to September. * Asterisks indicate species with very few records, where phenology was therefore estimated from the literature (Benton 2012, Fischer et al. 2016).

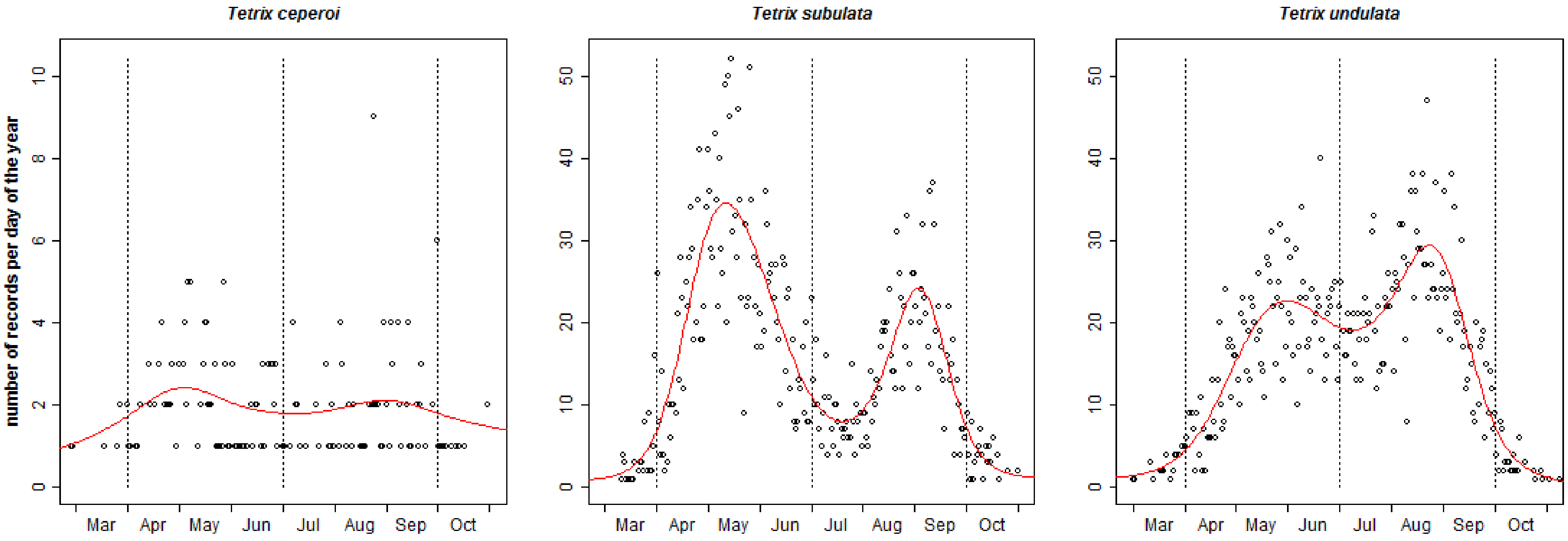
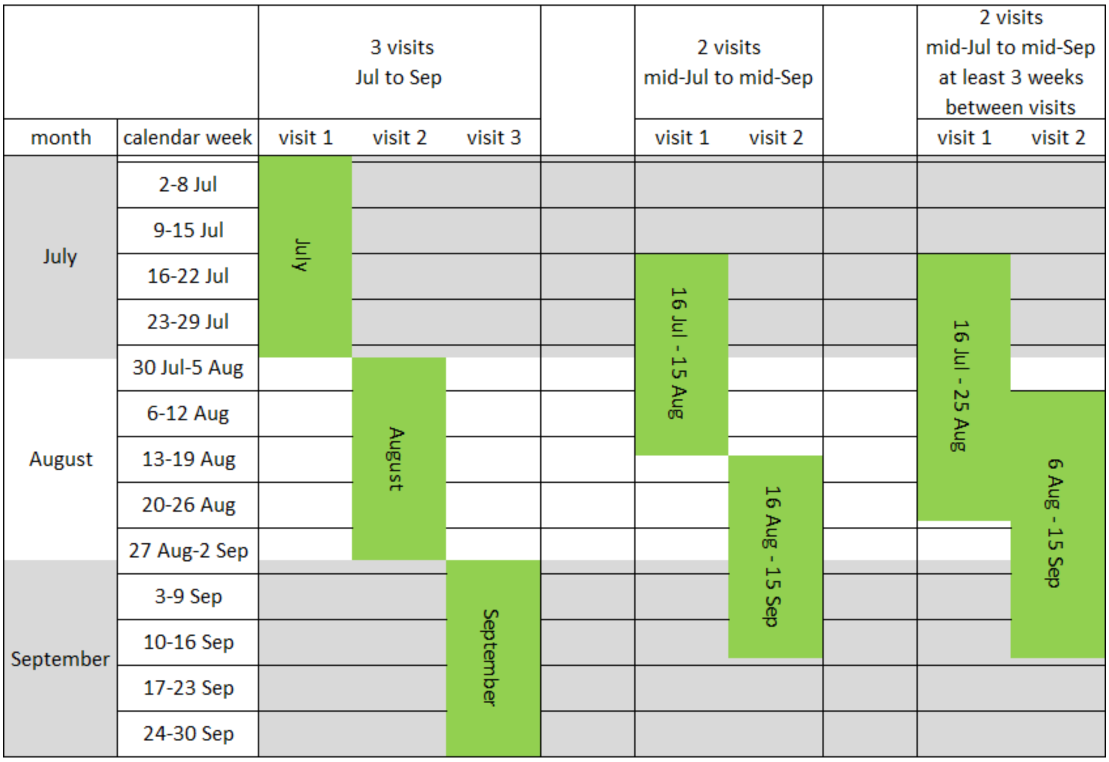


Fig. 5.2: Phenology of groundhoppers (Tetrigidae) in Britain.

Circles indicate total numbers of records per day of the year between 1980 and 2015. Red lines are fitted values of Generalised Additive Models (GAMs) with a thin plate regression spline smooth term, fitted in the R package "mgcv", version 1.8-12 (Wood 2011). Dashed lines mark the periods April to July and July to September.

Sampling during the period July to September would therefore cover all species except the two rare cricket species with spring peak abundances. If only two visits are carried out a narrower window from mid-July to mid-September would increase the overlap between the periods of peak abundance of bush-crickets and grasshoppers. Three example options for timing of monitoring visits are illustrated in Fig. 5.3. Timings should be both simple to communicate to recorders and leave as much flexibility as possible. Timing options could be evaluated further once pilot study data is available.

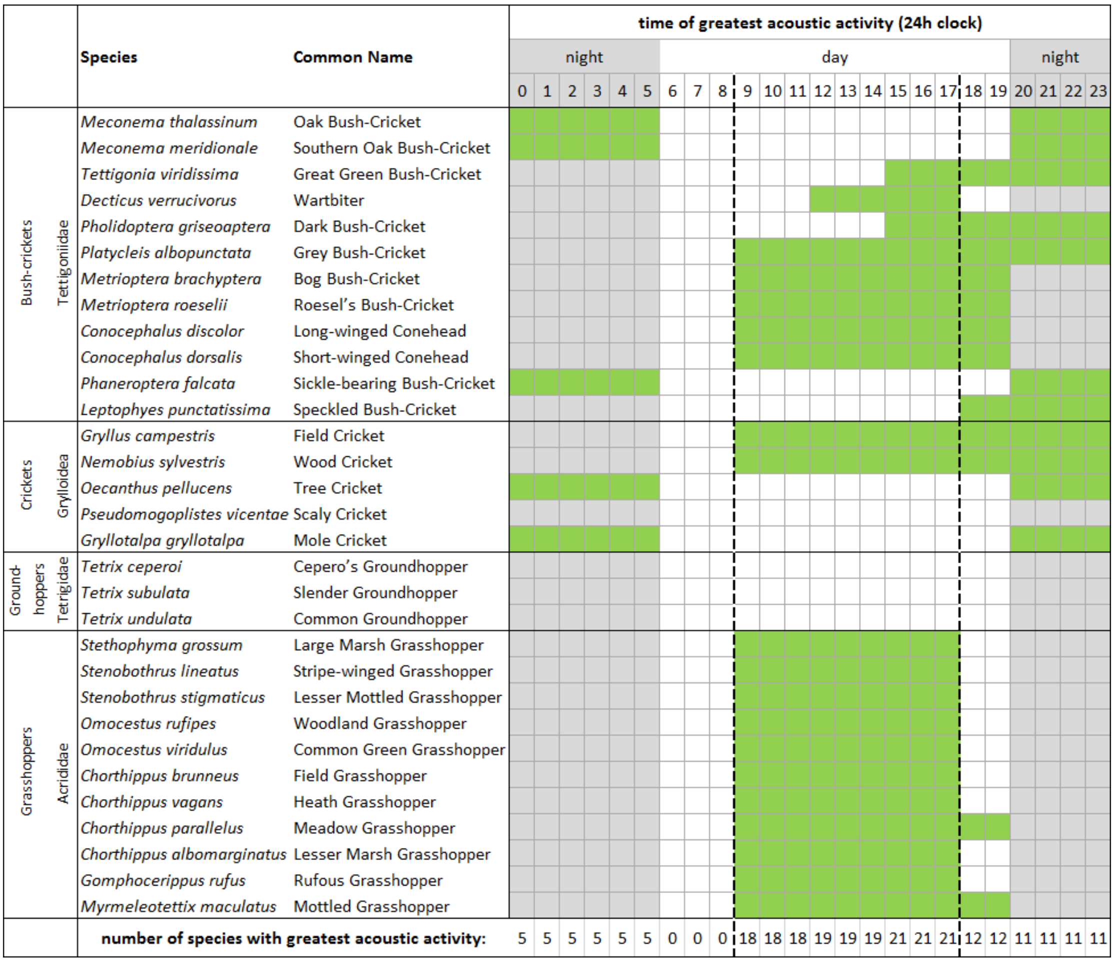


		3 visits Jul to Sep				2 visits mid-Jul to mid-Sep			2 visits mid-Jul to mid-Sep at least 3 weeks between visits	
month	calendar week	visit 1	visit 2	visit 3		visit 1	visit 2		visit 1	visit 2
July	2-8 Jul	July								
	9-15 Jul	🟩								
	16-22 Jul	🟩				16 Jul - 15 Aug			16 Jul - 25 Aug	
	23-29 Jul	🟩				🟩			🟩	
August	30 Jul-5 Aug		August			🟩			🟩	
	6-12 Aug		🟩			🟩			🟩	6 Aug - 15 Sep
	13-19 Aug		🟩			🟩	16 Aug - 15 Sep		🟩	🟩
	20-26 Aug		🟩				🟩		🟩	🟩
	27 Aug-2 Sep		🟩				🟩			🟩
September	3-9 Sep			September			🟩			🟩
	10-16 Sep			🟩			🟩			🟩
	17-23 Sep			🟩						
	24-30 Sep			🟩						

Fig. 5.3: Example options for timing of surveys for 2-3 annual visits.

5.3.3 Time of day

As ectothermic insects, Orthoptera rely on minimum ambient temperatures for their activity (Ingrisch and Köhler 1998). Highest activity, including stridulation, tends to occur during the warmest part of the day for grasshoppers (Acrididae) and other species of open grassland habitats. For many crickets (Grylloidea) and bush-crickets (Tettigoniidae) which inhabit taller vegetation where differences between day and night temperatures are less pronounced, peak activities occur during the second half of the afternoon and the first half of the night, particularly in periods when night temperatures are high (Nielsen and Dreisig 1970, Ingrisch and Köhler 1998). Times of greatest singing activity of the British species are summarised in Fig. 5.4.



		Species	**Common Name**	**time of greatest acoustic activity (24h clock)**																							
				night						day														night			
				0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Bush-crickets	Tettigoniidae	*Meconema thalassinum*	Oak Bush-Cricket	🟩	🟩	🟩	🟩	🟩	🟩															🟩	🟩	🟩	🟩
		Meconema meridionale	Southern Oak Bush-Cricket	🟩	🟩	🟩	🟩	🟩	🟩															🟩	🟩	🟩	🟩
		Tettigonia viridissima	Great Green Bush-Cricket																🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
		Decticus verrucivorus	Wartbiter													🟩	🟩	🟩	🟩	🟩	🟩						
		Pholidoptera griseoaptera	Dark Bush-Cricket																🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
		Platycleis albopunctata	Grey Bush-Cricket										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
		Metrioptera brachyptera	Bog Bush-Cricket										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩				
		Metrioptera roeselii	Roesel's Bush-Cricket										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩				
		Conocephalus discolor	Long-winged Conehead										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩				
		Conocephalus dorsalis	Short-winged Conehead										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩				
		Phaneroptera falcata	Sickle-bearing Bush-Cricket	🟩	🟩	🟩	🟩	🟩	🟩															🟩	🟩	🟩	🟩
		Leptophyes punctatissima	Speckled Bush-Cricket																			🟩	🟩	🟩	🟩	🟩	🟩
Crickets	Grylloidea	*Gryllus campestris*	Field Cricket										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
		Nemobius sylvestris	Wood Cricket										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
		Oecanthus pellucens	Tree Cricket	🟩	🟩	🟩	🟩	🟩	🟩															🟩	🟩	🟩	🟩
		Pseudomogoplistes vicentae	Scaly Cricket																								
		Gryllotalpa gryllotalpa	Mole Cricket	🟩	🟩	🟩	🟩	🟩	🟩															🟩	🟩	🟩	🟩
Ground-hoppers	Tetrigidae	*Tetrix ceperoi*	Cepero's Groundhopper																								
		Tetrix subulata	Slender Groundhopper																								
		Tetrix undulata	Common Groundhopper																								
Grasshoppers	Acrididae	*Stethophyma grossum*	Large Marsh Grasshopper										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩						
		Stenobothrus lineatus	Stripe-winged Grasshopper										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩						
		Stenobothrus stigmaticus	Lesser Mottled Grasshopper										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩						
		Omocestus rufipes	Woodland Grasshopper										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩						
		Omocestus viridulus	Common Green Grasshopper										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩						
		Chorthippus brunneus	Field Grasshopper										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩						
		Chorthippus vagans	Heath Grasshopper										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩						
		Chorthippus parallelus	Meadow Grasshopper										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩				
		Chorthippus albomarginatus	Lesser Marsh Grasshopper										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩						
		Gomphocerippus rufus	Rufous Grasshopper										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩						
		Myrmeleotettix maculatus	Mottled Grasshopper										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩				
		number of species with greatest acoustic activity:		5	5	5	5	5	5	0	0	0	18	18	18	19	19	19	21	21	21	12	12	11	11	11	11

Fig. 5.4: Times of day of greatest acoustic activity of Orthoptera.

Green shading indicates times of greatest acoustic activity (Fischer et al. 2016). Dashed lines indicate the period 9:00 to 18:00. Grey shading indicates approximate times from sunset to sunrise (20:00 to 6:00), corresponding to conditions in southern Britain in the second half of August.

Surveys conducted between 9:00 and 18:00 would therefore cover times of peak acoustic activity for the greatest numbers of species: all grasshoppers, two out of four crickets which sing, and five out of 12 bush-crickets which produce sounds. Three further bush-crickets sing during part of this time: the rare Wartbiter has peak activities in the afternoon from about 12:00 to 18:00, and Dark and Great Green Bush-crickets begin to sing from about 15:00, carrying on into the night. Oak and Southern Oak Bush-crickets produce sounds during the night, but these are extremely quiet (created by tapping a leg on a leaf) and not suitable for auditory monitoring in any case.

This leaves four sound-producing species (Sickle-bearing and Speckled Bush-cricket, as well as Tree and Mole Cricket) for which periods of peak acoustic activity would not be covered at all by surveys between 9:00 and 18:00. With the exception of the Speckled Bush-cricket all of these are currently extremely rare in Britain. For these four species, as well as Dark and Great Green Bush-crickets, surveys between sunset and midnight would best cover periods of peak acoustic activity. It is worth noting that existing structured monitoring schemes for other taxonomic groups do not necessarily cover all species, for example the UK Butterfly Monitoring Scheme (UKBMS) does not optimally record hairstreaks (Theclinae), and uses a range of additional methods for these species, e.g. larval and egg counts for some species (Brereton et al. 2016). Similarly, the UK Breeding Bird Survey (BBS) does not record breeding populations well for nocturnal owls (Strigiformes) and several species where counts are likely to include large numbers of non-breeding, wintering or migratory individuals (Harris et al. 2016).

5.3.4 Field methods

No one single field method is suitable for sampling abundance of all Orthopteran species in Britain (Gardiner et al. 2005). Acoustic counts are suitable for estimating abundance of males of most species and have high detection probabilities provided the species is active, because songs of most species can be heard over several meters in many different habitats (Fischer et al. 1997). Acoustic counts along transects are particularly suitable for quick, relative abundance sampling: recording effort can be standardised by the length of transects, and counting ‘on the go’ is time-efficient (Penone et al. 2013, Jeliazkov et al. 2016). Furthermore, Orthopteran distributions are often locally clumped, and transect counts are less likely to miss clumps than point surveys (Gardiner et al. 2005). Ultrasound (“bat”) detectors are frequently used as an aid for acoustic sampling of Orthoptera, allowing detection of higher frequency stridulations, and at greater distances than by the unaided ear (Ingrisch and Köhler 1998). For acoustic counts to be comparable between recorders, use of bat detectors needs to be standardised.

Quadrat searches are suitable for species that inhabit short or medium-height vegetation (i.e. not scrub or trees), which can be searched visually and allow placing of quadrats on the ground, and this method is not dependent on acoustic activity. Quadrats can be open or “box quadrats” (also called biocenometers), i.e. with high sides (>50cm) which prevent escape of insects. Leaving aside mark-release-recapture methods, which are likely to be relatively unpopular for volunteer surveys due to their very time-consuming nature, box quadrats have been found to be the most accurate method for estimating abundances in habitats with suitable vegetation for their use (Gardiner and Hill 2006, Fischer et al. 2016).

Beating is suitable for species inhabiting tall herbaceous and woody vegetation, and like other active search methods, is not dependent on acoustic activity. It is quick and simple, and standardised beating (standard number of taps, standard beating tray size) has been used for relative abundance assessments of Orthoptera of these habitats such as the Oak bush-cricket *Meconema thalassinum* (Ausden 1996, Ingrisch and Köhler 1998).

Sweep-netting has also been successfully used as a method for sampling Orthoptera, but catches have been found to vary significantly depending on sweep net height above the ground, speed and arc length, so these parameters need to be standardised carefully; in addition, as with quadrat searches, sweep netting is not suitable for tall vegetation (O'Neill et al. 2002, Gardiner et al. 2005). Sweep netting is particularly suitable for the silent and inconspicuous groundhoppers (Tetrigidae), which usually inhabit very short vegetation or open ground (Benton 2012). Pitfall trapping is suitable for a minority of ground-dwelling species only (Schirmel et al. 2010).

Fig. 5.5 provides an overview of the suitability of sampling methods for Orthoptera in Britain. Suitability was considered good (++) where methods are mentioned as suitable for abundance monitoring in the literature cited above for the main habitats in which species occur, and limited (+) where reservations are expressed about suitability of the method, or about its use in some of the species’ habitats.

Overall, assuming surveys are conducted between 9:00 and 18:00, a combination of acoustic counts, box quadrats and beating would provide suitable methods for recording abundances of all species except the rare habitat specialists Scaly and Mole Cricket, and limited suitability for three species with greatest acoustic activity after 18:00 only, Dark, Tree, and Sickle-bearing Bush-cricket (the latter two currently extremely rare in Britain). Acoustic counts after sunset would provide the greatest additional benefit, but are probably not suitable for a volunteer scheme. Whether volunteers are willing to carry box quadrats will have to be evaluated; to be suitable, quadrats need to be light-weight, for example foldable bamboo frames covered with white canvass (Fischer et al. 2016). On the upside, box quadrats reward recorders with good views of the species (Gardiner and Hill 2006), and folded quadrats can act as beating trays.

It is proposed to only count adults, because identification of nymphs can be difficult (Evans and Edmondson 2007), and because only adults will be detected by acoustic counts, i.e. counts between different methods will be more comparable if only adults are counted. If surveys are conducted during July to September, an exception will be made for groundhoppers, which will be immature or subadult at that time; groundhoppers do not stridulate so will not be detected by acoustic counts and the question of comparability of methods does not arise.

Table 5.1: Suitability of field methods for recording abundance of Orthopteran species.

		Species	Common name	acoustic count 9:00 – 18:00	acoustic count 20:00 – 24:00	box quadrat	open quadrat	sweep-netting	beating	pitfall trapping
Bush-crickets	Tettigoniidae	*Meconema thalassinum*	Oak Bush-Cricket						++	
		Meconema meridionale	Southern Oak Bush-Cricket						++	
		Tettigonia viridissima	Great Green Bush-Cricket	+	++	+			+	
		Decticus verrucivorus	Wartbiter	++		++	+			
		Pholidoptera griseoaptera	Dark Bush-Cricket	+	++				+	
		Platycleis albopunctata	Grey Bush-Cricket	++	++	+	+	+		
		Metrioptera brachyptera	Bog Bush-Cricket	++		+	+			
		Metrioptera roeselii	Roesel's Bush-Cricket	++		++	+	+		
		Conocephalus dorsalis	Short-winged Conehead	++		+	+	+		
		Conocephalus fuscus	Long-winged Conehead	++		+	+	+		
		Phaneroptera falcata	Sickle-bearing Bush-Cricket		++	+	+	+	+	
		Leptophyes punctatissima	Speckled Bush-Cricket		++				++	
Crickets	Grylloidea	*Gryllus campestris*	Field Cricket	++	++	+	+	+		
		Nemobius sylvestris	Wood Cricket	++	++	+	+			
		Oecanthus pellucens	Tree Cricket		++	+	+	+	+	
		Pseudomogoplistes vicentae	Scaly Cricket				+			++
		Gryllotalpa gryllotalpa	Mole Cricket		++					
Ground-hoppers	Tetrigidae	*Tetrix ceperoi*	Cepero's Groundhopper			++	+	++		+
		Tetrix subulata	Slender Groundhopper			++	+	++		+
		Tetrix undulata	Common Groundhopper			++	+	++		+
Grasshoppers	Acrididae	*Stethophyma grossum*	Large Marsh Grasshopper	++		++	+	+		
		Stenobothrus lineatus	Stripe-winged Grasshopper	++		++	+	+		
		Stenobothrus stigmaticus	Lesser Mottled Grasshopper	++		++	+	+		
		Omocestus rufipes	Woodland Grasshopper	++		+		+	+	
		Omocestus viridulus	Common Green Grasshopper	++		++	+	+		
		Chorthippus brunneus	Field Grasshopper	++		++	+	+		
		Chorthippus vagans	Heath Grasshopper	++		+		+	+	
		Chorthippus parallelus	Meadow Grasshopper	++		++	+	+		
		Chorthippus albomarginatus	Lesser Marsh Grasshopper	++		++	+	+		
		Gomphocerippus rufus	Rufous Grasshopper	++		++	+	+	+	
		Myrmeleotettix maculatus	Mottled Grasshopper	++		++	+	+		+
		No. of species for which suitability of method is:	**good**	**19**	**9**	**14**		**3**	**3**	**1**
			limited	**2**		**11**	**23**	**18**	**7**	**4**

Suitability of methods for abundance detection: ++ good, + limited, blank = not suitable.

5.3.5 Weather conditions

Insect activity and detectability strongly depend on ambient temperatures (Pollard 1977, Ingrisch and Köhler 1998). Weather during monitoring visits should therefore be as warm and sunny as possible, with standard minimum conditions. The UK Butterfly Monitoring Scheme, which runs from April to September, stipulates temperatures of 13°C or higher (and, between 13 and 17°C, sunshine for at least 60% of the time), maximum wind speeds of 5 on the Beaufort scale (38km/h), and no rain. For Orthoptera monitoring during July to September, higher minimum requirements are likely to be useful, and feasible: over the past 30 years (1987-2016) mean and maximum Central England Temperatures during September (the coolest month of the July-September period) have been about 5°C higher than during April (the coolest month in the April-September period) (Parker et al. 1992, Parker and Horton 2005). Therefore, a minimum of 18°C is proposed. High winds affect audibility of Orthoptera songs, and a previous acoustic survey required maximum wind speeds of 19km/h, i.e. 3 on the Beaufort scale, so the same restriction is proposed here (Fischer et al. 1997). These are preliminary proposals and will need to be evaluated during field trials. For all surveys, temperature, percentage sunshine and wind speed need to be recorded, and they may be used as covariates during data analysis.

5.3.6 Tie-in with existing surveys

It is proposed to carry out surveys on existing transects currently monitored for other species groups as part of the UK Butterfly Monitoring Scheme (UKBMS), Wider Countryside Butterfly Survey (WCBS) and Breeding Bird Survey (BBS). This has several advantages over establishing new sites and transects: Firstly, routes are already known and land-owner permissions in place where required: a survey of recorders for herptile monitoring found that needing to organise access permission and not knowing the site or area were the top factors discouraging participation (Stanbury et al. 2015). Secondly, there is potential to recruit volunteers from existing large recorder networks to monitor their sites for an additional species group; for example, many BBS recorders monitor mammals, dragonflies and butterflies along their transects. Thirdly, information about habitats and land use has often been recorded already at established sites. Finally, monitoring of different species groups at the same sites creates the potential for comparative and multi-taxon analyses.

5.3.7 Random sampling framework

In order to be representative, sampling sites need to be selected at random. However, a purely random selection of sites has the disadvantage of being likely to provide insufficient sample sizes for rare habitats, and too many survey sites in areas remote from cities and towns which volunteer recorders are unlikely to visit. Therefore, in order to ensure sufficient sample sizes across all habitats or other regions of interest while maximising participation, stratified random selection of sites has been chosen for several existing monitoring schemes, with stratification by environmental zones (Countryside Survey), by density of recorders (BBS/WCBS), or by habitat (National Plant Monitoring Scheme).

For Orthoptera monitoring, which has a relatively small pool of potential recorders compared to butterflies and birds, random selection and stratification by recorder density is proposed for transects on WCBS and on BBS sites, in order to maximise potential participation. For transects on UKBMS sites no random selection of sites is suggested, because the UKBMS itself is not randomised and most transects are on high quality semi-natural habitat and / or protected areas, where monitoring site conservation status is of interest in itself.

5.3.8 Summary of proposed survey method

The following preliminary survey method is proposed for Orthoptera monitoring. It will need to be trialled and evaluated during a pilot study.

- carry out three counts per year in July, August and September.
- walk transects between 9:00 and 18:00, recording start and end time.
- the weather should be as warm, sunny and still as possible (minimum temperature 18°C, maximum wind speed 3 on Beaufort scale); record temperature, wind speed, and percent sunshine.
- acoustic count: walk along transect with a bat detector, note species and numbers of all stridulating males you hear per section. On UKBMS transects, do not double-count singing individuals where transect sections are in close vicinity.
- box quadrats: at the start- and mid-point of each section carry out a box quadrat count, i.e. on WCBS / BBS transects one every 100m, 20 in total. Box quadrats 1x1m, 75cm high, search for 1 minute using a stick 75cm long to flush insects.
- beating: at the start- and mid-point of each section, beat the nearest trees or bushes for 1 minute and count Orthoptera dislodged. Beating tray 100x75cm (folded box quadrat), beating stick 75cm long. Omit if there are no trees / bushes within 15m.
- times taken for a BBS / WCBS transect (for UKBMS depends on length): approx. 45 minutes for each 1km transect, plus 20 quadrats + 20x beating = approx. 2:10h for whole transect

5.4 Sample acoustic transect count data collected 2016

In June-September 2016, a trial of acoustic transect counts with a bat detector was carried out at one UKBMS site in Oxfordshire (Swyncombe Downs SSSI) (Fig. 5.5). No beating or box quadrat counts were carried out. As expected, singing activity for grasshoppers (blues) started and peaked earlier than for bush-crickets (reds), with maximum numbers of both groups recorded during August. Maximum numbers heard during the period suggested for monitoring (July to September) ranged from 6 for Long-winged Conehead *Conocephalus discolor* to 60 for Common Green Grasshopper *Omocestus viridulus*, with an average maximum of 39.4 ± 18.3 across species. Mean numbers recorded during these months ranged from 3.4 ± 1.7 for *C. discolor* to 27.6 ± 18.1 for Meadow Grasshopper *Chorthippus parallelus*.

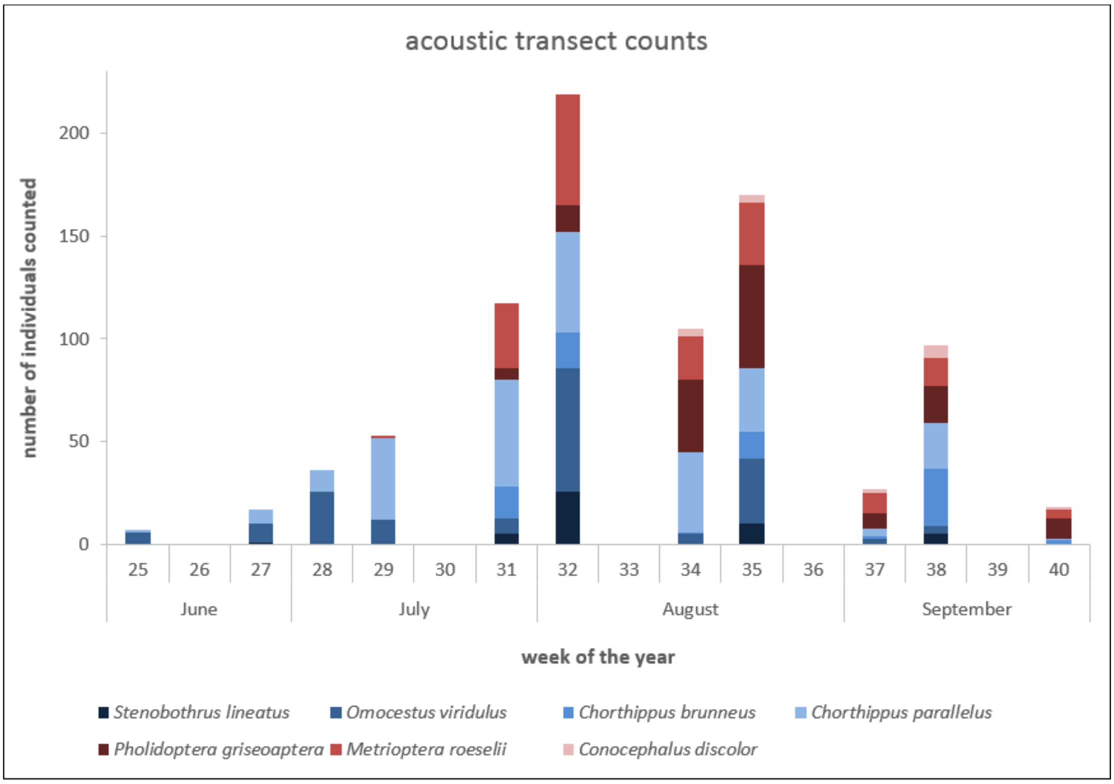


Fig. 5.5. Sample acoustic transect count data collected in 2016.

Numbers of male grasshoppers (blues) and bush-crickets (reds) heard stridulating along UKBMS Swyncombe Downs transect in 2016. Each stacked column represents a visit. No visits were carried out in weeks with no data, i.e. no samples had zero counts.

5.5 Power analysis

In order to estimate what population changes an Orthoptera abundance monitoring scheme might be able to detect, a power analysis was carried out. Long-term population dynamics of European Orthoptera have received relatively little study so far, perhaps because they currently have little economic impact, unlike Orthoptera in other parts of the world (Ingrisch and Köhler 1998). There is, therefore, limited information available for parameterising a power simulation, and the analysis presented here is preliminary, and is expected to be refined when additional data become available, for example from a pilot study trialling the monitoring method presented here.

5.5.1 Method

Statistical power to detect population trends was calculated in the following three steps: (1) Random count data with known properties were repeatedly generated for a range of different scenarios with different combinations of assumed values for (a) the mean starting count of study species; (b) the magnitude of population declines; (c) the variability in population numbers and sampling accuracy; and (d) the number of sites sampled. (2) Trends in these data were analysed with a method commonly used for existing insect monitoring scheme data. 3) Power for each scenario was calculated as the proportion of simulations for which a correct trend was detected.

Simulated count data were generated by adapting methods and code used for power analysis during design of the National Plant Monitoring Scheme (Pescott et al. 2015, Walker et al. 2015, Pescott et al. 2016): Count data for each study year were simulated as randomly generated numbers with Poisson distributions. The variability produced by pure Poisson distributions (with variance equal to mean) was insufficient to recreate realistic coefficients of variation (CVs, see below); therefore additional noise was introduced by adding randomly generated numbers with a normal distribution centred on zero to the mean counts for which Poisson distributions were to be generated, with the standard deviation of this normal distribution adjusted to produce desired overall CVs.

Starting counts (i.e. counts in the first study year) were assumed to be a mean of either 60 or 6 individuals. The former was taken to represent a transect count of an abundant species on a good-quality site: it was the maximum sample count for the most abundant species during trials on Swyncombe Downs SSSI UKBMS transect in 2016 (section 5.3). A count of 6 individuals was chosen to represent a rare species on a high quality site, or any species on a poor-quality “wider countryside” site such as a BBS or WCBS transect: 6 was the maximum count for the rarest species on Swyncombe Downs in 2016.

Population changes were assumed to be exponential, i.e. with a constant rate or proportion of change from year to year (Mace et al. 2008). Population count data were simulated with two levels of decline: a lower, 15% total decline over ten years (approximately 2% annual decline), and a greater, 30% total decline over ten years (4% annual decline). For comparison, abundances of wider countryside butterfly species in the UK have declined by 16% between 2005 and 2014, and butterflies on farmland in England by 37% over the same time period (Fox et al. 2015).

Three levels of assumed annual variability of populations and sampling were explored – “low”, “medium” and “high”. Values for the low variability scenario were based on values from Richards & Waloff’s 1947-51 study of five species of grasshopper at Silwood Park in Berkshire, UK, which is still the most detailed investigation of population dynamics of European Orthoptera (Richards and Waloff 1954, Ingrisch and Köhler 1998): Being based on a single site not subject to any major changes in management over the study period, and sampled intensively by professional researchers, the variability in population counts in this study was assumed to represent a “best case”, low variability scenario. CVs were calculated for annual total numbers of adults of Richards & Waloff’s study species, and averaged 0.6 for the most abundant species (Meadow and Field grasshoppers, *Chorthippus parallelus* and *brunneus*), and 0.7 for the least abundant (Mottled grasshopper, *Myrmeleotettix maculatus*). For the low variability scenario in the present study, therefore, the CV for populations of abundant species (starting count 60) was assumed to be 0.6, and for rare species (starting count 6) it was assumed to be 0.7, consistent with observations that counts of sparse populations tend to be subject to greater proportional variation (Ingrisch and Köhler 1998). For “medium” and “high” variability scenarios, higher coefficients of variation of 0.8 and 1.0 respectively were assumed for abundant species, and correspondingly greater values of 0.93 and 1.17 respectively for rare species – values similar to the high end of CVs for insects reported in a meta-analysis of a large number of long-term counts of local populations of 24 taxa (Gibbs et al. 1998). Simulated population counts were capped at ten times the starting number in order to prevent individual unrealistically large values affecting results (Pescott et al. 2015). All analyses were carried out in the software environment R (R Core Team 2016).

Declines in the simulated data were analysed with log-linear Poisson regression models as performed by the R implementation of the statistical software TRIM (package “rtrim” (Bogaart et al. 2016)). TRIM (“Trends and Indices for Monitoring Data”) is widely used for analysis of monitoring scheme data, including the UK Butterfly Monitoring Scheme, the Rothamsted Insect Survey, the European Grassland Butterfly Indicator, and the UK Breeding Bird Survey (Conrad et al. 2004, UKBMS 2006, BTO 2011, van Swaay et al. 2015). TRIM can impute missing values (not required here) and then fits a generalised linear model (GLM) with a Poisson error structure and logarithmic link to annual abundances, allowing for differences between sites. There are options to take into account serial correlation (non-independence of counts at the same site in different years) and overdispersion (counts being more variable than a pure Poisson distribution would suggest), both of which were employed here.

Simulations were run for a range of 2 to 500 sites (at increments of 2 sites in order to keep computing times manageable), and repeated 500 times. For each given number of sites, statistical power was then calculated as the proportion of simulations for which the models detected a significant negative trend. A LOWESS smoother was fitted to the estimates of power, and minimum numbers of sites required for achieving 80% power to detect changes were derived from these smoothed values (Cleveland 1981).

5.5.2 Results

Estimates of statistical power for different scenarios are illustrated in Fig. 5.6., with vertical dashed lines indicating minimum numbers of sampling sites required to achieve 80% power. Results suggest that for abundant species on good quality habitat (with an assumed starting count of 60 individuals), between 24 and 52 sites would be needed to detect a 30% decline over ten years, depending on the variability of populations and sampling accuracy. For rare species on good quality sites, or species on poor quality habitat (with an assumed starting count of 6 individuals), slightly higher numbers of between 30 and 80 sites would be needed to detect such a 30% decline. The power analyses suggest that considerably higher numbers of sites would be required to reliably detect smaller declines of 15% over ten years: between 90 and 244 sites for abundant species on good quality habitat, and between 126 and 364 sites for rare species or poor quality habitats, depending on the variability of populations and sampling accuracy.

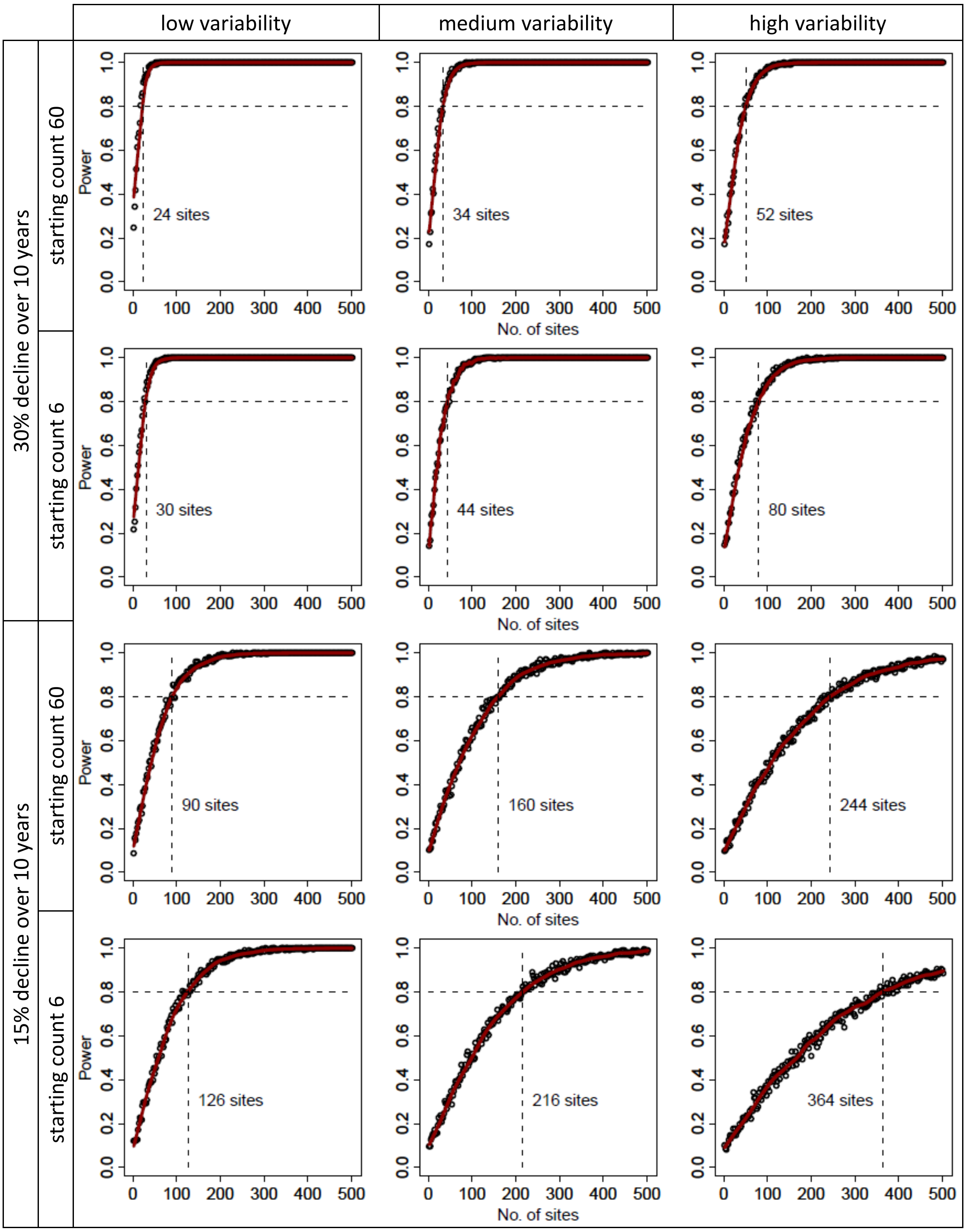


Fig. 5.6: Estimated power to detect declines over ten years, depending on the assumed variability of population numbers and sampling accuracy, magnitude of declines, size of starting populations, and numbers of sampling sites.

Black circles indicate estimates of power for a given number of sites, and red lines show LOWESS smoothers. Vertical dashed lines indicate minimum numbers of sampling sites required to achieve 80% power (horizontal dashed lines).

5.6 Discussion

Rapid climatic and land use changes are affecting many regions and habitats, and there is an urgent need to monitor species' populations in order to understand differences in how species are affected, and be able to base conservation decisions on good evidence, and monitor responses to interventions (Sutherland et al. 2004, Hayhow et al. 2016). Britain is fortunate in having a strong tradition of biological recording by volunteers, and distributions of many species groups including Orthoptera have been monitored for several decades through unstructured recording by volunteers. However, systematic monitoring of abundances is only carried out for few species groups, particularly among invertebrates. Where abundance monitoring data exists, it has proved invaluable in assessing the conservation status of species, identifying drivers of decline, and investigating wider biological and ecological questions. Rigorous abundance monitoring protocols are likely to reduce the number of potential recorders, and survey designs need to strike a careful balance between the quality and quantity of data collected. This chapter has aimed to develop a preliminary protocol for Orthoptera abundance monitoring suitable for volunteer participation, which is enjoyable and not too onerous to take part in, and able to sample abundances of as many Orthopteran species as possible.

Thorough field trials of the proposed method will be required in order to evaluate sampling variability and accuracy, and assess whether recorders find the method practicable and enjoyable, and if there are aspects which need revision. A pilot study could compare transect counts with absolute population estimates of adults obtained through mark-release-recapture counts in order to assess the accuracy of sampling – for example, how closely transect counts are correlated with absolute population estimates over the course of the emergence period (Pollard and Yates 1993). Similarly, the gains to be achieved through greater recording effort (more frequent transect counts, greater numbers of box quadrat counts per transect) could be assessed (Roy et al. 2007). Differences between recorders could be investigated by carrying out counts on the same transects on the same days.

Counts of seasonal invertebrates have been evaluated by estimating the area under the emergence curve for each species at each site, for example by using Generalised Additive Models to fit a smoothed line, allowing interpolation of any missing counts (Rothery and Roy 2001). With reduced sampling of three visits per year as proposed here, this will not be possible, and a covariate for time of year (such as calendar week) could be included in analyses in order to account for variation in abundances over the season (Roy et al. 2007). It would therefore be useful to survey a few sites more intensively, in order to be able to estimate and account for annual variation in phenology; alternatively, phenology could be estimated from unstructured distribution records with life stage information (Roy et al. 2007, Bishop et al. 2013). It is increasingly becoming possible to include other covariates in analyses as well, for example conditions on the day of sampling such as survey time and weather, and environmental information such as climate and land cover (Hochachka et al. 2012, Dennis et al. 2016). Such advances in modelling techniques are likely to improve accuracy of estimates further in future, but will also require more input data; this will need to be considered in detail before a recording method is rolled out, so that information is recorded as required and recording is as “future proof” as possible.

There is a level of duplication in the proposed design in that many species are sampled by both acoustic counts and box quadrats (Table 5.1). However, the methods complement each other, and there are advantages to having both. The combination of both methods provides greater species coverage: acoustic counts are more suitable for several bush-cricket species, which inhabit tall vegetation, while box quadrats may detect groundhoppers (Tetrigidae), which do not stridulate. Acoustic counts allow rapid and efficient survey of large areas because species can be detected at distances of several meters, provided they are stridulating. Box quadrats sample much smaller areas, but are not as activity-dependent as acoustic counts. A combination of acoustic and visual counts could also be important for providing an enjoyable recording experience to recorders. Finally, for species which are sampled well by both methods, employing both may allow assessment of detectability of one method by using the counts of the other (Pellet et al. 2012).

Estimated numbers of sites required to detect declines for different types of species produced in the power analysis here (section 5.4.2) broadly agree with estimates produced for a national pollinator monitoring scheme, which suggested that between 20 and 75 sites would be needed to detect 30-50% changes over ten years for common species (Carvell et al. 2016). However, the numbers of the low and medium variability scenarios are lower than those of a power analysis for a 3-visit scheme produced by sub-sampling actual monitoring data of the 26-visit UK Butterfly Monitoring Scheme, which concluded that for univoltine species with a single peak of adult activity in the summer (which many Orthoptera in Britain are (Beckmann et al. 2015)), an average of 261 sites would be required to detect a 25% decline in abundance over 10 years, and an average of 45 sites to detect a 50% decline (Roy et al. 2007). Only the high variability scenarios here produced similar estimates, suggesting that for a volunteer-based survey which encompasses a large variety of sites this is a more realistic assumption for variability of population counts than the medium- and low-variability scenarios. In the context of the proposed monitoring scheme, medium or low count variability is perhaps likely to occur only for abundant species on nature reserves which are under consistent long-term management, and sampled by professional staff. Results from a pilot study of the proposed method could be used to parameterise and revise the power analysis.

The numbers of recorders an Orthoptera abundance monitoring scheme attracts and retains, and therefore the types of species and magnitudes of declines it can expect to monitor successfully, will depend on factors including how enjoyable or onerous the protocol is perceived to be, and how much organisational support is provided, including feedback and training for recorders (Tweddle et al. 2012, Pocock et al. 2015b, Stanbury et al. 2015). If participation is low, a focus on regions or habitats could reduce variation between sites and hence provide better estimates, and the method could also be useful for monitoring of individual important sites in a standardised way. On a large scale, the usefulness of an abundance monitoring method will depend on the accuracy of sampling it achieves, and the level of participation over time and space. The method proposed here will need to be evaluated and refined through field trials and feedback from recorders, in order to strike the best balance between encouraging wide use and collecting accurate data. If it manages to do both, it can greatly support the study and effective conservation of an important and popular group of insects with the help and involvement of a wider public.

6. General Discussion

6.1 Summary of main findings

This thesis had two main aims: (1) to investigate interspecific differences in recent range changes of Orthoptera in Britain, and effects of climatic change and climatic variability on the pattern and process of range expansion of two rapidly expanding species, and (2) to review and evaluate the available Orthoptera recording data in Britain, and the scope for development and expansion of Orthoptera monitoring in future in order to maximise its usefulness for conservation and research.

In chapter 2, I critically reviewed the Orthoptera Recording Scheme and its data, and the application of statistical methods for distribution trend analysis. I found that over five decades of operation since 1968, the scheme's practices of record notation and sharing have evolved considerably, and in combination with the absence of standardisation and measures of recording effort this has led to a range of biases in the data collected. Several statistical methods for distribution trend analysis that take such biases into account are available, but care is needed with the selection of methods and setup of analyses in order to meet the assumptions made.

In chapter 3, I employed one of these methods to calculate distribution trends for Orthopteran species in Britain, and linked them to their biological traits in order to understand whether traits explain interspecific differences in responses to climate and land use change. I found large changes in the distributions of some species, and positive relationships between three traits and range change that accord well with the nature of recent environmental changes: ranges tended to increase for habitat generalists, species that oviposit in the vegetation above ground, and for those with a southerly distribution. However, the trait effects applied mainly just to two species, *Conocephalus discolor* and *Metrioptera roeselii*, which had shown the greatest range increases. I concluded that trait-based analyses may contribute to understanding interspecific differences in responses to environmental change, but results need to be interpreted with caution and may have limited predictive power beyond the study system.

In chapter 4, I assessed the influence of seasonal weather on the range expansion process of these two rapidly spreading species, specifically on (1) annual colonisation rates, calculated from distribution monitoring data, and on (2) incidence of dispersive individuals near the range margins, sampled in field surveys. I found that colonisation rates were higher for both species in years when weather was both warm and wet during the period of juvenile development, and colonisation rates were also positively associated with warm (and dry, for *C. discolor*) weather during the period of adult dispersal and reproduction. There was some limited evidence for similar effects of seasonal weather on the incidence of macropterous individuals in *C. discolor*, but not for *M. roeselii*. The findings suggest that annual variations in seasonal weather significantly influence range expansion rates, and that the study species are likely to undergo waves of expansion in climatically favourable years. This may increase successful establishment of new populations through greater numbers of colonists, and may also be advantageous in fragmented landscapes, allowing species to invest in dispersal only sporadically and under favourable conditions. The findings also highlight the importance of considering interactive effects of temperature and precipitation.

In chapter 5, I assessed the feasibility of structured Orthoptera abundance and site monitoring by volunteers, with a view to improving available data quality for, and the potential scope of, a broad range of future research. Based on literature, existing data, and a first trial of methods, a protocol is proposed which should be able to sample abundances of most species and be suitable for volunteers. The protocol consists of three daytime acoustic transect counts on existing butterfly or bird monitoring sites in July, August and September, with stops for carrying out box quadrat and beating counts. A power analysis suggested that 35-45 sites will be needed to detect large, 30% declines over 10 years, and 150-220 sites to detect smaller, 15% declines. Structured abundance monitoring of Orthoptera in Britain therefore looks feasible, but comprehensive field trials will be required in order to evaluate sampling variability and accuracy of the proposed protocol, and assess whether it is practicable and enjoyable for recorders.

In the following, I briefly reflect on these findings together, on some ideas for follow-on research, and on developments of Orthoptera recording by volunteers and the role of the data produced in future research.

6.2 Future research, and the role of citizen science data

The investigations of effects of species traits and seasonal weather on range changes are both correlative analyses, with measures of range change and colonisation rate related to explanatory variables in regression models. While the results can suggest likely underlying mechanisms and have been interpreted in light of existing mechanistic studies, additional studies will be useful to corroborate and explore the findings presented here further (Hanski 2015). The nature of the Orthoptera recording scheme data makes analysis most robust when summed at large temporal and spatial scales (chapter 2) and therefore most suitable for broad, correlative studies. Availability of rigorous, site-specific abundance data collected with a standard protocol would increase the opportunity for more detailed, mechanistic investigations. For example, abundance data would allow further investigation of the effects of population density on macropterism across species' ranges. Availability of abundance data would also increase the opportunities for other research areas, such as fluctuations of populations in response to weather and natural enemies, and generally allow closer linkage of observed changes in distributions to processes of population dynamics. This may be particularly useful, because both the investigations of trait effects on range change (chapter 3) and of seasonal weather effects on the range expansion process (chapter 4) highlighted that the factors influencing range changes are complex, and their effects frequently combine and interact. A combination of abundance data with distribution data might therefore allow more detailed investigation and understanding of this complexity.

6.2.1 Stochastic range expansion

The finding that seasonal weather significantly affects colonisation rates, leading to stochastic spread, has been little investigated so far to my knowledge, and has potential importance for understanding species' spread through fragmented landscapes (chapter 4). Further investigations would therefore be of interest. Additional stochastic weather parameters likely to influence dispersal and / or colonisation could be considered, such as droughts or floods during the period of juvenile development, or the occurrence of southerly winds during the period of adult dispersal.

My finding of a significant interaction between the effects of warmth and rainfall on distributional changes has also received little study so far to my knowledge and further investigations would be of interest. For example, interactions between different seasonal weather parameters, or between the effects of spring and autumn weather could be considered.

While I investigated here only the *temporal* pattern of spread, a study of the *spatial* pattern could corroborate findings and consider other factors in addition, and investigate some of the ideas raised: if range expansions can be modelled in a way that takes temporal and spatial variations in recording effort into account – for example using dynamic occupancy or spatial survival models (Purse et al. 2015) – it would become possible to test whether differences in environmental conditions such as local climate or land cover influence which areas are colonised first. A spatial model of spread might also allow investigation of the importance of habitat fragmentation. Such an investigation would be helped by a study of gradients in habitat associations across species' ranges (Oliver et al. 2012).

6.2.2 Further investigations of macropterism

Establishment of an abundance monitoring scheme for Orthoptera would create opportunities for a variety of future research (chapter 5). For example, if population densities as well as incidence of wing morphs are recorded during visits (the latter during box quadrat counts), a clearer large-scale picture of density effects on macropterism might emerge.

It is currently unclear at what point in the season macropters disperse – only at the start of, or throughout, their adult lives. It is generally thought that dispersal occurs early in the adult season (Ingrisch and Köhler 1998), but there is little concrete evidence. Perhaps this could be investigated with a mark-release-recapture study to compare recovery rates of macropters and brachypters over a season. Such a study could perhaps be coupled with genetic tests to establish whether macropterous adults are of local origin or have flown in (Hochkirch and Damerau 2009), or it might be possible to permanently mark developing juveniles.

6.2.3 Future perspectives for distribution monitoring

Over five decades of operation since 1968 the Orthoptera Recording Scheme has successfully built up and maintained a pool of recorders, coordinators, and data, with numbers of incoming records roughly level at approximately 3,000 per annum since 1990 (Fig. 2.12). The scheme has successfully developed with the times, and with the iRecord online system and the iRecord Grasshoppers mobile app has efficient and convenient routes for data collection, submission and curation in place. The new sound recording functionality of the app is an exciting development that should facilitate submission and verification of additional records, and the bat detector function provides low-cost access to a powerful technological recording aid to recorders (Fig. 2.4). There are therefore good prospects for the recording scheme's future. Nevertheless, the scope for further evolution and optimisation could be explored, with the aim of maintaining and further developing the balance between satisfaction for recorders and users of data (Preston et al. 2012).

6.2.3.1 Recording of complete lists and absences

As discussed in chapter 2, occupancy detection models are the most powerful and robust current method for distribution trend analysis for species with sufficient quantity and quality of data (Isaac et al. 2014), and they are likely to be increasingly used in future for data analysis and conservation status assessments. A key assumption occupancy models make is that species are recorded against a full list, in order to infer non-detections of species. It would therefore be useful to encourage recorders to consistently survey sites for all species of the group and mark records as such when they have done so. The iRecord Grasshoppers app multi-species recording form allows recorders to do so by ticking a box indicating a full list (Fig. 2.4). However, it is receiving very little use so far. Other citizen science projects have been very successful in encouraging recording of complete lists, for example the "e-bird" project: the majority of records are now submitted as checklists, and throughout the project records are referred to as "checklists" rather than sightings or records (http://ebird.org). In the Orthoptera scheme, recording of complete lists could be encouraged further in a number of ways, from giving it an increased profile in scheme communications, to adding information to the online recording form, and making the multi-species recording form the default in the app. In addition to recording of full lists, the recording scheme could explore ways to allow recorders to make "absence records", i.e. indicate explicitly when they have surveyed an area for a species and *not* found it.

However, the lack of prescriptiveness is a strength of current recording that allows new recorders to become involved and make first contributions, so any changes would have to be introduced carefully and be well explained. Offering different levels of participation may be the best way (Pescott et al. 2015), and encourage recorders to progress from submission of single records to submission of complete lists, and potentially to structured abundance monitoring.

6.2.4 Future perspectives for abundance monitoring, sound recording and classification

If the abundance monitoring protocol developed in chapter 5 is successfully field-tested, and deemed suitable for wider use by volunteers, in its current form or with amendments, this could mark an important advance for the study and conservation of Orthoptera in Britain. One of the key recommendations of the recently published first European Red List of Orthoptera is the development of a pan-European monitoring programme for Orthoptera (Hochkirch et al. 2016), and experience from development and field testing of this protocol could potentially contribute to this goal.

A complementary development might be the integration of sound recording and automated sound classification. Automatic classification (i.e. identification) of species sounds has been the subject of research for more than a decade (Chesmore and Ohya 2004, Riede et al. 2006). Classifications are still prone to large errors for many species, but are beginning to become more precise with quantifiable levels of accuracy: a recent study of bush-crickets in Britain achieved greater than 85% accuracy (counting both false negatives and false positives) for two out of six species (Newson et al. 2017), while another study in France achieved greater than 90% accuracy (not counting false negatives) for two species analysed (Jeliazkov et al. 2016). Developments in recording technology, sound libraries (Riede et al. 2006, Baker et al. 2015, Cigliano et al. 2017) and classification algorithms are set to continue and are likely to make collection and processing of very large bioacoustic datasets more feasible in future.

It is therefore likely that it will become possible to combine abundance monitoring data collected by recorders along a transect with information from automated, continuous monitoring at one or several points along the transect. Due to the high current cost of recording devices, and since each device can only monitor a small surrounding area, it would not be practical to monitor an entire site with automated devices (Newson et al. 2017). However, if recording devices are deployed at one or several points along a transect, these could provide precise measures of seasonal and daily activity patterns of Orthoptera, by which transect counts covering the whole site could then be weighted.

A further possibility is to make audio recordings of Orthoptera calls in a standardised way during each monitoring visit, for example by carrying a light-weight recorder along transects (Zilli et al. 2014). Perhaps the sound recording function of the iRecord Grasshoppers app could be used for this purpose, if the quality of recordings provided by different mobile devices using the app is comparable (perhaps with a low-cost standardised external microphone). Recordings made during transect counts would allow quality control of counts, resulting in greater standardisation across sites, particularly if recordings are analysed in an automated or semi-automated way. Archiving of such recordings would allow standardised automated analysis across years and sites with improved algorithms developed in future. Ways to integrate sound recording into the current protocol could be explored as part of a pilot study.

6.3 Outlook

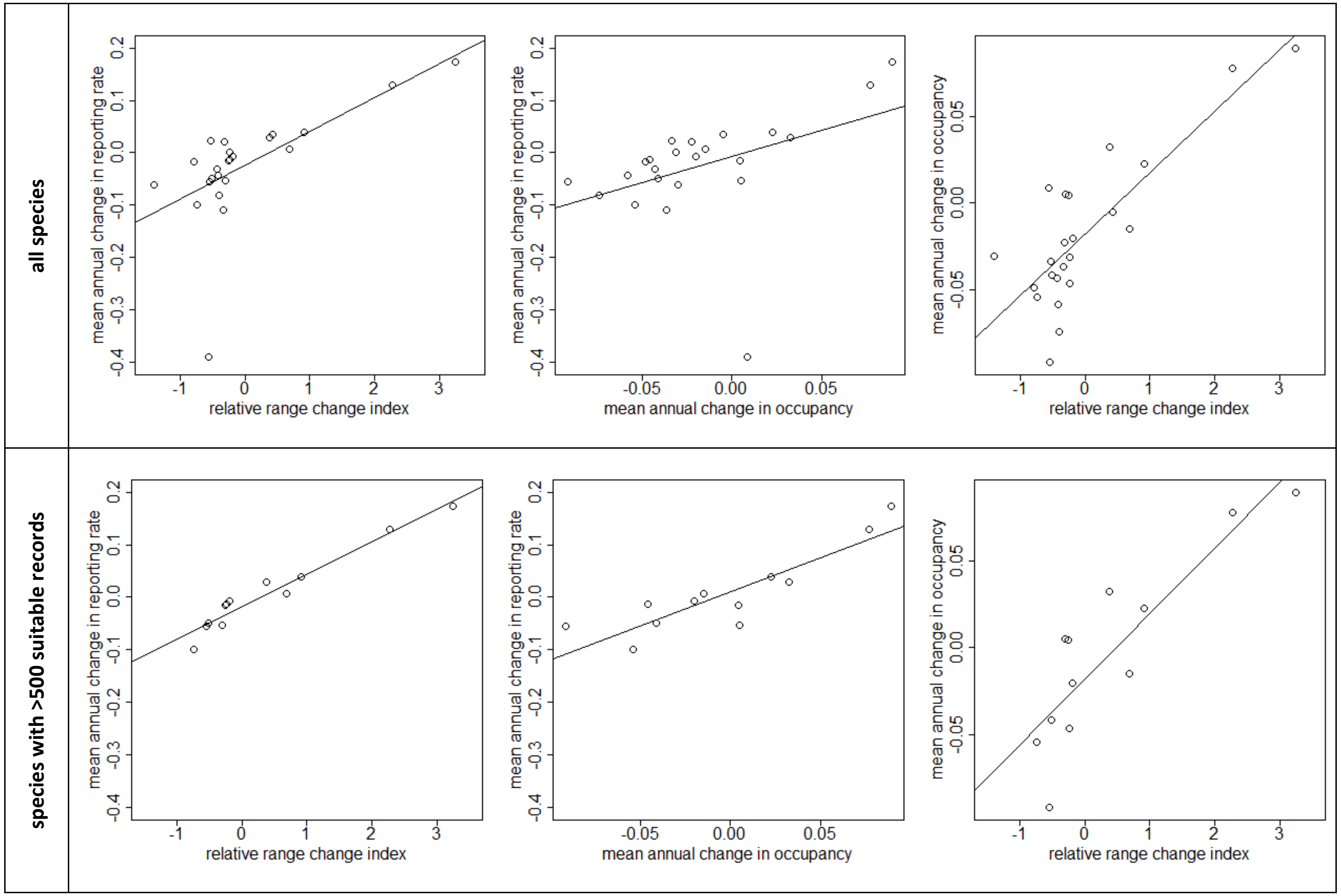
Climate and land use changes are set to continue throughout this century and beyond, with expected ongoing impacts on species' distributions, highlighting the importance of monitoring and study of distributional change to inform conservation. The recently published first European Red List of Orthoptera classed more than 25% of Orthopteran species in Europe as Threatened, making Orthoptera the most endangered group of terrestrial invertebrates assessed so far (Hochkirch et al. 2016). At the same time, as this thesis has shown, a proportion of species are expanding their distributions rapidly, which will change community compositions in the future. It is hoped that the findings of this thesis contribute to the understanding of interspecific differences in distributional change, and of the underlying processes, and will inform and facilitate further research in future. Biological recording by members of the public will continue to be important in this process – both as an effective way of gathering data, and as a way of fostering involvement of people with nature and an understanding of the living world.

Appendix to Chapter 2

S 2.1 Table: Results for three distribution trend measures for Orthoptera in Britain, 1980-2009

	relative range change index			**reporting rate model**						**occupancy detection model**			number of records used in reporting rate and occupancy models
				mean annual change in detection probability (on logit scale)			no. of species recorded per visit (list length)			mean annual change in occupancy (on logit scale)			
species	no. squares period 1	no. squares period 2	relative range change index	estimate	SE	significance	estimate	SE	significance	estimate	SE	significance	
Meconema thalassinum	325	317	-0.30	-0.053	0.005	***	0.262	0.026	***	0.005	0.015		1,198
Tettigonia viridissima	145	135	-0.42	-0.043	0.017	*	0.773	0.080	***	-0.059	0.011	***	369
Pholidoptera griseoaptera	419	424	-0.19	-0.008	0.006		0.559	0.030	***	-0.020	0.008	*	2,107
Platycleis albopunctata	56	55	-0.40	-0.080	0.025	**	0.621	0.100	***	-0.074	0.030	*	222
Metrioptera brachyptera	74	70	-0.43	-0.030	0.021		0.635	0.104	***	-0.043	0.012	***	223
Metrioptera roeselii	73	352	2.27	0.128	0.008	***	0.649	0.038	***	0.078	0.010	***	1,563
Conocephalus discolor	46	406	3.24	0.174	0.009	***	0.591	0.036	***	0.089	0.014	***	1,147
Conocephalus dorsalis	139	218	0.43	0.036	0.015	*	0.718	0.064	***	-0.005	0.009		487
Leptophyes punctatissima	351	451	0.38	0.029	0.005	***	0.437	0.026	***	0.032	0.013	*	2,186
Nemobius sylvestris	17	19	-0.31	0.022	0.036		0.397	0.162	*	-0.023	0.019		55
Tetrix ceperoi	25	27	-0.33	-0.109	0.042	*	0.540	0.161	***	-0.036	0.016	*	58
Tetrix subulata	175	302	0.69	0.006	0.009		0.332	0.038	***	-0.015	0.013		554
Tetrix undulata	314	315	-0.24	-0.013	0.008		0.552	0.040	***	-0.046	0.016	**	782
Stethophyma grossum	14	7	-1.40	-0.061	0.057		0.847	0.274	**	-0.031	0.018		33
Stenobothrus lineatus	70	76	-0.24	0.001	0.021		0.874	0.096	***	-0.031	0.012	*	226
Omocestus rufipes	51	38	-0.78	-0.016	0.024		0.508	0.092	***	-0.049	0.016	**	156
Omocestus viridulus	417	372	-0.50	-0.049	0.007	***	0.596	0.037	***	-0.041	0.011	**	1,330
Chorthippus brunneus	576	525	-0.54	-0.055	0.005	***	0.827	0.032	***	-0.092	0.029	**	2,960
Chorthippus vagans	6	6	-0.56	-0.389	0.002	***	1.679	0.002	***	0.009	0.007		24
Chorthippus parallelus	541	533	-0.24	-0.014	0.005	**	0.955	0.036	***	0.004	0.011		3,167
Chorthippus albomarginatus	126	264	0.92	0.039	0.009	***	0.790	0.051	***	0.023	0.011		999
Gomphocerippus rufus	27	25	-0.53	0.023	0.035		0.522	0.145	***	-0.034	0.014	*	98
Myrmeleotettix maculatus	219	166	-0.74	-0.099	0.014	***	0.966	0.071	***	-0.055	0.011	***	631

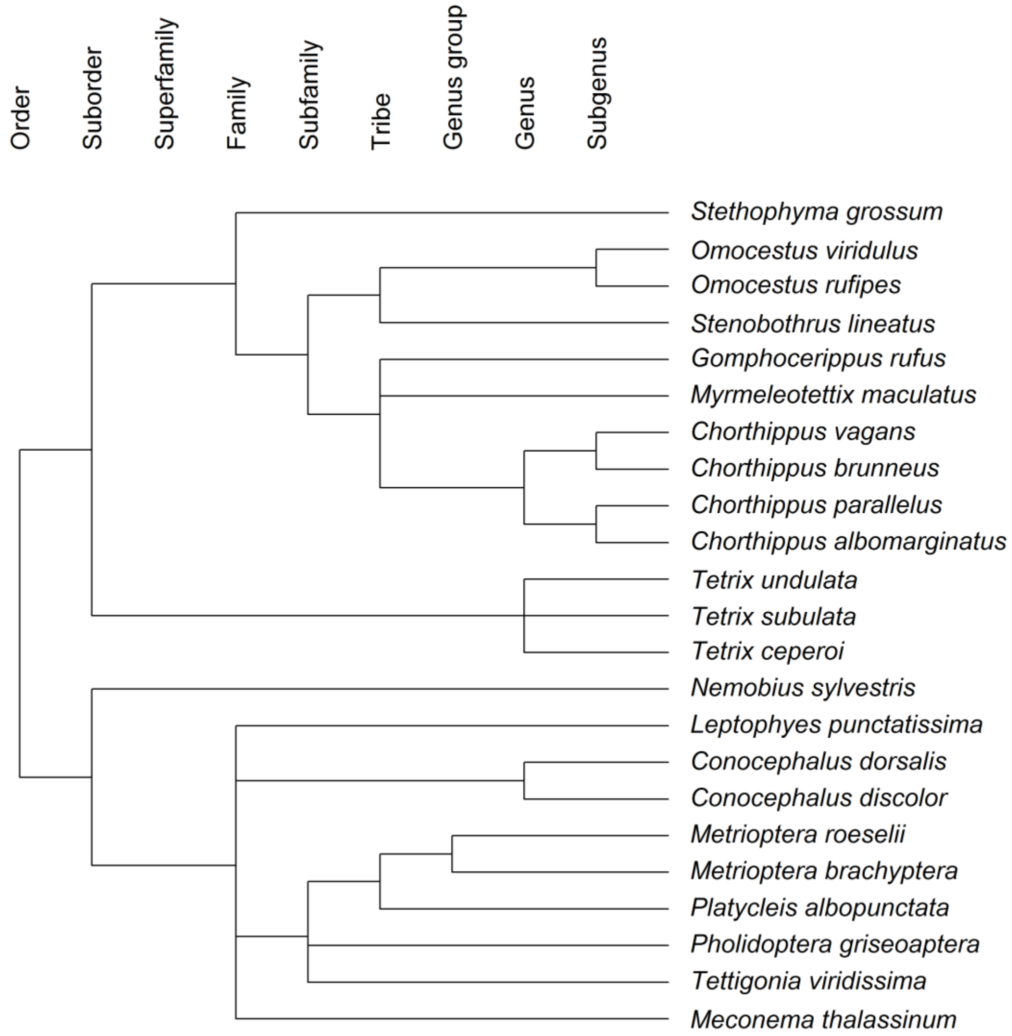
Red shading indicates negative trend estimates, green shading positive. The relative range change index has no measure of significance for individual species' indices. For reporting rate and occupancy models significance of trend estimates is indicated by asterisks (* P<0.05, ** P<0.01, *** P<0.001). Species for which a relative range change index could not be calculated are excluded, i.e. species occurring in 5 or fewer surveyed hectads in the 1980-9 time period.



S 2.1 Fig.: Pairwise comparison of three distribution trend measures.

Distribution trend estimates are compared for all species (top), and for species a minimum of 500 suitable records for reporting rate and occupancy models (bottom). Solid lines indicate linear models. Axis scales have been kept identical to facilitate comparison. For detailed distribution trend values see S 2.1 Table.

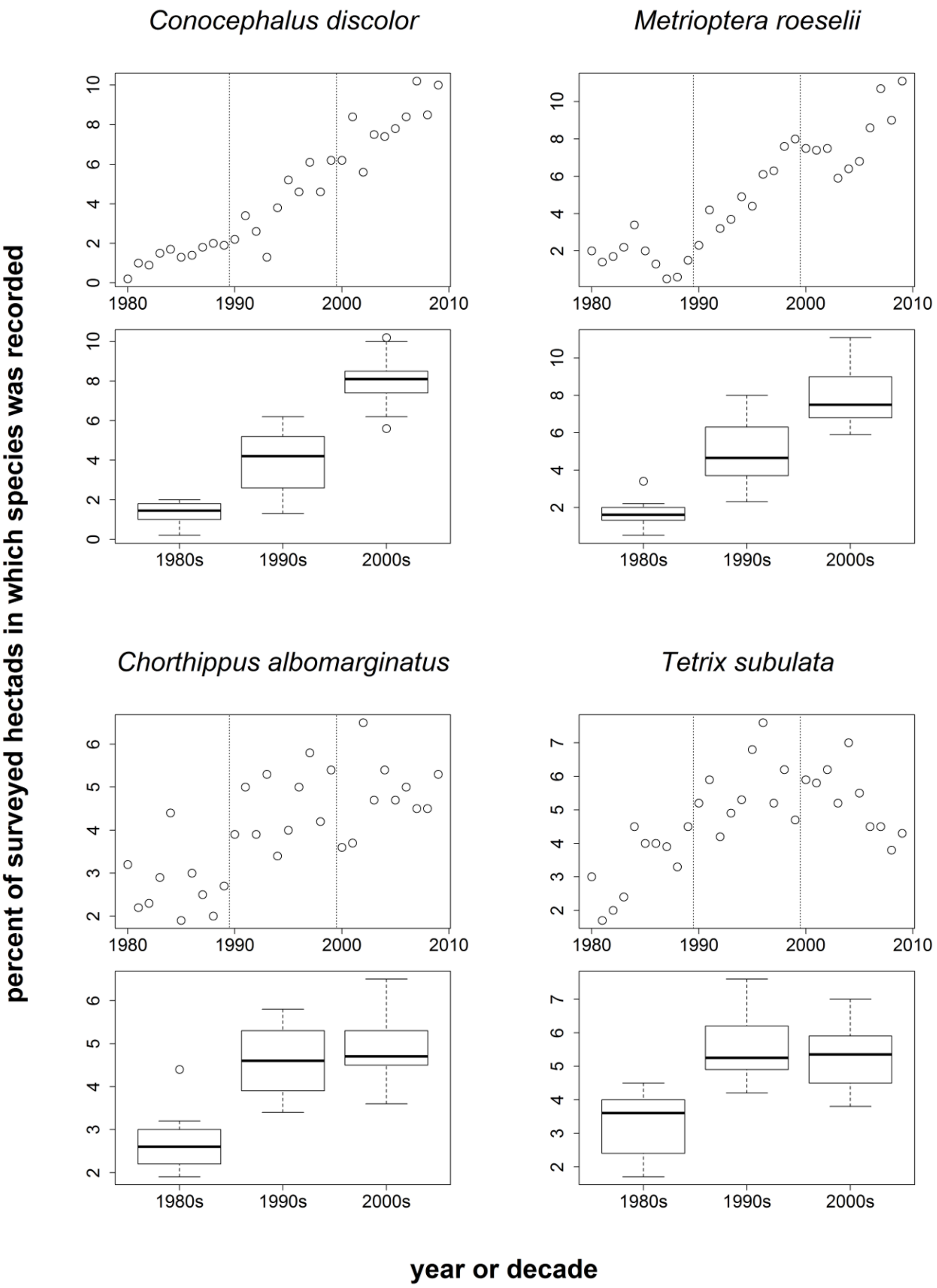
Appendix to Chapter 3



S 3.1 Fig. "Working phylogeny" of grasshoppers and related species in Britain.

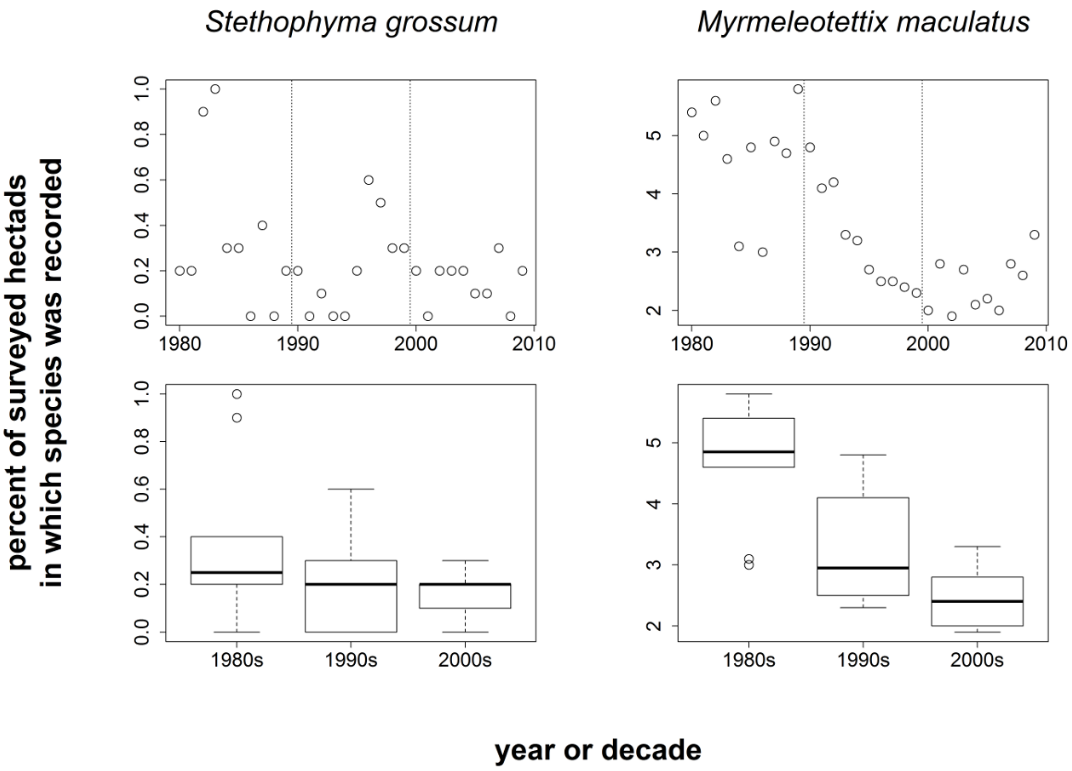
In the absence of a comprehensive phylogeny of the study species, this "working phylogeny" was approximated based on taxonomic divisions according to the Orthoptera Species File, with all branch segment lengths assumed to be equal (Grafen 1989, Eades et al. 2013).

N.B.: In keeping with currently prevailing use in Britain and in line with the rest of the text, some species names have been altered from the Orthoptera Species File, and subgenus names are not included: *Omocestus (Omocestus) viridulus = Omocestus viridulus; Omocestus (Omocestus) rufipes = Omocestus rufipes; Chorthippus (Glyptobothrus) vagans = Chorthippus vagans; Chorthippus (Glyptobothrus) brunneus = Chorthippus brunneus; Chorthippus (Chorthippus) parallelus = Chorthippus parallelus; Chorthippus (Chorthippus) albomarginatus = Chorthippus albomarginatus; Conocephalus (Anisoptera) dorsalis = Conocephalus dorsalis; Conocephalus (Xiphidion) fuscus = Conocephalus discolor; Roeseliana roeselii = Metrioptera roeselii.*



S 3.2 Fig. Scatter- and boxplots of annual relative numbers of hectad records for species with the greatest positive range changes.

To account for changes in overall recording effort, annual numbers of hectads in which a species was recorded were calculated as a percentage of the total number of hectads surveyed in the respective year.



S 3.3 Fig. Scatter- and boxplots of annual relative numbers of hectad records for species with the greatest negative range changes.

To account for changes in overall recording effort, annual numbers of hectads in which a species was recorded were calculated as a percentage of the total number of hectads surveyed in the respective year.

S 3.1 Table. Grasshopper and related species range changes between 1980-9 and 2000-9.

Range sizes and “uncorrected” and “corrected” range change values for four levels of recording effort.

	based on hectads with >=1 species recorded in both time periods					based on hectads with >=2 species recorded in both time periods					based on hectads with >=3 species recorded in both time periods					based on hectads with >=4 species recorded in both time periods				
species	no. of 10km squares occupied 1980-9	no. of 10km squares occupied 2000-9	"uncorrected range change"	"corrected range change" , all species	"corrected range change" , excluding *C. discolor* and *M. roeselii*	no. of 10km squares occupied 1980-9	no. of 10km squares occupied 2000-9	"uncorrected range change"	"corrected range change" , all species	"corrected range change" , excluding *C. discolor* and *M. roeselii*	no. of 10km squares occupied 1980-9	no. of 10km squares occupied 2000-9	"uncorrected range change"	"corrected range change" , all species	"corrected range change" , excluding *C. discolor* and *M. roeselii*	no. of 10km squares occupied 1980-9	no. of 10km squares occupied 2000-9	"uncorrected range change"	"corrected range change" , all species	"corrected range change" , excluding *C. discolor* and *M. roeselii*
Meconema thalassinum	315	294	-0.11	-0.34	-0.41	277	247	-0.20	-0.46	-0.68	247	216	-0.26	-0.48	-0.72	215	193	-0.24	-0.47	-0.71
Tettigonia viridissima	139	125	-0.13	-0.43	-0.39	127	112	-0.16	-0.47	-0.47	118	107	-0.13	-0.41	-0.34	113	99	-0.18	-0.48	-0.52
Pholidoptera griseoaptera	405	401	-0.02	-0.19	-0.18	353	360	0.05	-0.09	0.02	317	318	0.01	-0.07	0.03	263	274	0.14	0.07	0.34
Platycleis albopunctata	52	49	-0.06	-0.43	-0.16	50	48	-0.04	-0.39	-0.1	48	44	-0.10	-0.47	-0.25	46	40	-0.16	-0.54	-0.41
Metrioptera brachyptera	74	68	-0.09	-0.44	-0.26	64	63	-0.02	-0.34	-0.03	57	56	-0.02	-0.35	-0.05	49	50	0.02	-0.30	0.08
Metrioptera roeselii	71	332	1.95	2.31	-	70	278	1.88	2.17	-	64	241	1.88	2.10	-	60	206	1.85	2.05	-
Conocephalus discolor	46	378	2.63	3.23	-	42	331	2.79	3.36	-	38	293	2.91	3.39	-	36	253	2.96	3.45	-
Conocephalus dorsalis	137	213	0.55	0.48	1.53	131	186	0.48	0.37	1.31	119	158	0.40	0.27	1.09	108	140	0.39	0.24	1.05
Leptophyes punctatissima	337	424	0.42	0.39	1.1	315	380	0.45	0.44	1.2	280	335	0.51	0.56	1.43	240	290	0.65	0.71	1.77
Nemobius sylvestris	18	19	0.05	-0.36	0.24	17	19	0.11	-0.27	0.42	17	19	0.11	-0.31	0.33	16	18	0.12	-0.28	0.4
Tetrix ceperoi	25	27	0.08	-0.30	0.29	25	26	0.04	-0.34	0.19	24	25	0.04	-0.36	0.13	23	24	0.04	-0.34	0.17
Tetrix subulata	171	282	0.68	0.67	1.87	156	241	0.65	0.61	1.79	136	212	0.70	0.67	1.9	126	180	0.60	0.53	1.63
Tetrix undulata	309	298	-0.06	-0.27	-0.26	270	267	-0.02	-0.21	-0.15	229	236	0.06	-0.07	0.17	205	203	-0.02	-0.20	-0.1
Stethophyma grossum	14	7	-0.67	-1.40	-1.9	14	6	-0.82	-1.57	-2.32	13	6	-0.75	-1.49	-2.12	13	6	-0.75	-1.46	-2.1
Stenobothrus lineatus	68	72	0.06	-0.24	0.18	59	64	0.09	-0.20	0.28	55	58	0.06	-0.25	0.17	51	50	-0.02	-0.36	-0.05
Omocestus rufipes	49	37	-0.29	-0.74	-0.81	43	36	-0.19	-0.60	-0.5	37	32	-0.15	-0.57	-0.42	33	32	-0.03	-0.41	-0.06
Omocestus viridulus	402	350	-0.25	-0.51	-0.85	307	266	-0.28	-0.54	-0.9	261	215	-0.39	-0.63	-1.07	211	178	-0.35	-0.62	-1.03
Chorthippus brunneus	553	500	-0.27	-0.50	-0.98	452	428	-0.21	-0.40	-0.8	389	367	-0.29	-0.40	-0.84	324	319	-0.11	-0.19	-0.42
Chorthippus vagans	6	6	0.00	-0.54	0.14	6	6	0.00	-0.52	0.16	6	6	0.00	-0.58	0.01	6	6	0.00	-0.54	0.09
Chorthippus parallelus	526	503	-0.11	-0.29	-0.5	459	438	-0.19	-0.37	-0.75	398	377	-0.30	-0.40	-0.88	334	320	-0.33	-0.49	-1.12
Chorthippus albomarginatus	123	241	0.85	0.87	2.37	114	203	0.78	0.76	2.18	101	179	0.80	0.77	2.19	94	153	0.72	0.65	1.98
Gomphocerippus rufus	27	25	-0.08	-0.51	-0.17	24	23	-0.04	-0.45	-0.05	22	22	0.00	-0.43	0.01	21	22	0.05	-0.35	0.18
Myrmeleotettix maculatus	206	157	-0.34	-0.70	-1.04	173	134	-0.34	-0.69	-1.02	154	118	-0.37	-0.69	-1.01	134	96	-0.48	-0.84	-1.34

S 3.2 Table. Results of Grubbs' tests for outliers.

		“uncorrected range change”				“corrected range change”			
		level of recording effort (minimum number of species recorded in “surveyed squares”)				level of recording effort (minimum number of species recorded in “surveyed squares”)			
		1	2	3	4	1	2	3	4
Conocephalus discolor	G	3.25	3.38	3.42	3.47	3.20	3.33	3.35	3.41
	p	0.0018	0.0007	0.0005	0.0003	0.0025	0.0010	0.0009	0.0006
Metrioptera roeselii	G	3.43	3.38	3.34	3.33	3.32	3.26	3.20	3.19
	p	0.0004	0.0005	0.0007	0.0008	0.0009	0.0014	0.0021	0.0022

Test statistics (G) and p-values (p) for “uncorrected” and “corrected range change” and four levels of recording effort. In each case, *Conocephalus discolor* and *Metrioptera roeselii* were identified as outliers.

S 3.3 Table. Results of Shapiro-Wilk tests for normality of residuals.

			test statistic W			p-value			
	range change measure	recording effort level	min	median	max	min	median	max	% of p-values >= 0.05
models with <u>all species</u>	“uncorrected”	1	0.906	0.957	0.974	0.033	0.405	0.790	98
		2	0.929	0.961	0.982	0.104	0.480	0.935	100
		3	0.918	0.962	0.985	0.060	0.506	0.974	100
		4	0.932	0.968	0.985	0.122	0.631	0.975	100
	“corrected”	1	0.913	0.958	0.974	0.048	0.418	0.789	98
		2	0.921	0.961	0.977	0.069	0.488	0.844	100
		3	0.919	0.960	0.983	0.063	0.468	0.945	100
		4	0.936	0.960	0.980	0.147	0.454	0.911	100
models with species <u>excluding *C. discolor* and *M. roeselii*</u>	“uncorrected”	1	0.855	0.924	0.977	0.005	0.104	0.871	81
		2	0.881	0.949	0.978	0.016	0.327	0.890	96
		3	0.907	0.944	0.978	0.048	0.266	0.897	98
		4	0.938	0.967	0.987	0.195	0.671	0.988	100
	“corrected”	1	0.863	0.924	0.978	0.007	0.104	0.896	91
		2	0.895	0.955	0.978	0.028	0.420	0.889	98
		3	0.909	0.949	0.980	0.053	0.320	0.921	100
		4	0.942	0.971	0.991	0.239	0.764	0.998	100

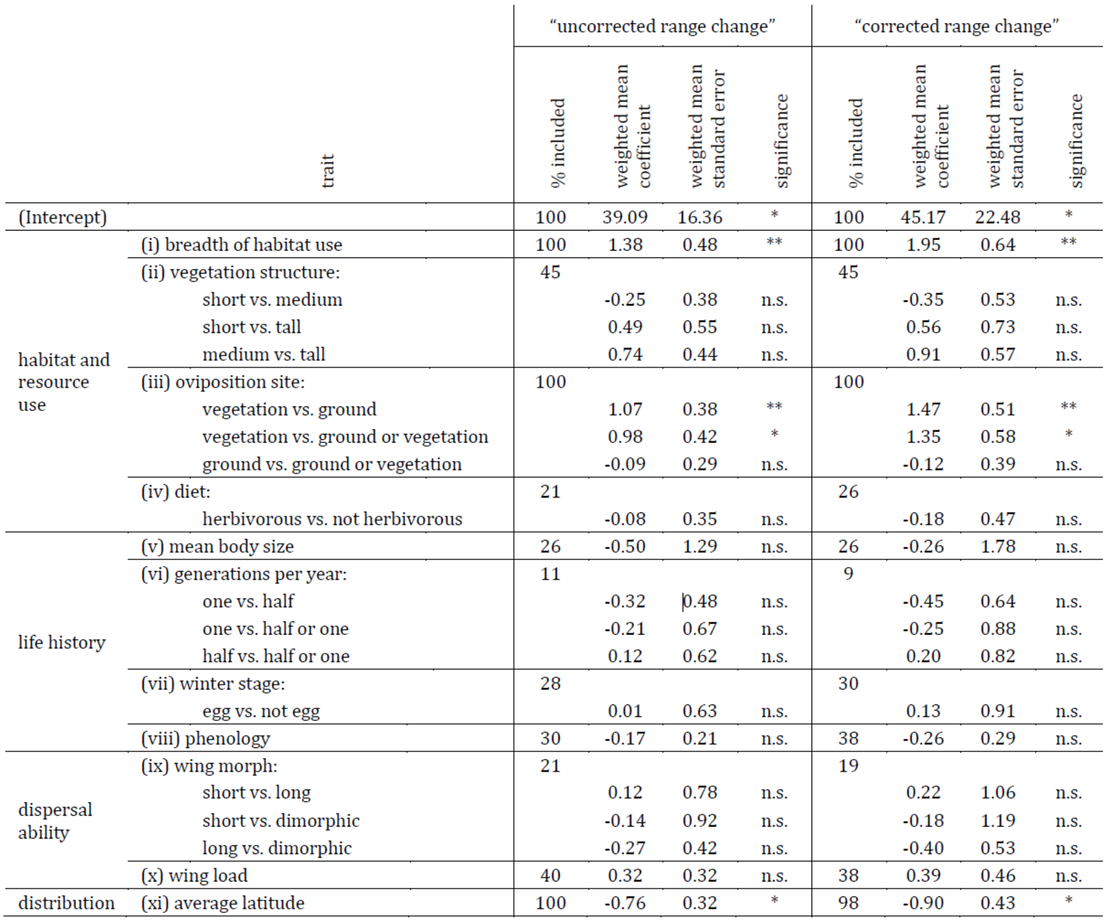
Minima, medians and maxima of Shapiro-Wilk test statistic W and associated p-values, testing for normality of residuals of top GLM model sets with ΔAIC<4 for two range change measures and four levels of recording effort. Results for models with all species (top half of table) and models with species excluding *Conocephalus discolor* and *Metrioptera roeselii* (bottom half).

S 3.4 Table. Moran's I phylogenetic autocorrelation indices and associated p-values.

	range change measure	recording effort level	Moran's I min	Moran's I median	Moran's I max	p-value min	p-value median	p-value max	% of p-values >= 0.05
models with <u>all species</u>	"uncorrected"	1	0.084	0.112	0.132	0.040	0.066	0.132	96
		2	0.086	0.112	0.132	0.040	0.067	0.126	96
		3	0.084	0.102	0.174	0.008	0.086	0.131	98
		4	0.086	0.099	0.116	0.063	0.092	0.122	100
	"corrected"	1	0.075	0.109	0.129	0.044	0.073	0.158	98
		2	0.073	0.110	0.129	0.041	0.071	0.164	95
		3	0.080	0.099	0.119	0.046	0.093	0.141	98
		4	0.081	0.097	0.112	0.054	0.098	0.138	100
models with species <u>excluding *C. discolor* and *M. roeselii*</u>	"uncorrected"	1	0.087	0.126	0.194	0.010	0.055	0.131	56
		2	0.102	0.131	0.200	0.007	0.049	0.096	46
		3	0.101	0.129	0.201	0.007	0.054	0.096	58
		4	0.103	0.133	0.209	0.006	0.051	0.099	51
	"corrected"	1	0.088	0.122	0.186	0.013	0.060	0.132	65
		2	0.105	0.129	0.193	0.009	0.053	0.090	58
		3	0.103	0.131	0.198	0.009	0.051	0.094	50
		4	0.109	0.128	0.206	0.007	0.058	0.090	65

Minima, medians and maxima for top GLM model sets with ΔAIC<4 for two range change measures and four levels of recording effort. Results for models with all species (top half of table) and models with species excluding *Conocephalus discolor* and *Metrioptera roeselii* (bottom half).

S 3.5 Table. Impacts of species traits on distribution changes of British grasshoppers and crickets (all species) between the 1980s and 2000s, phylogenetic models.



		“uncorrected range change”				“corrected range change”			
	trait	% included	weighted mean coefficient	weighted mean standard error	significance	% included	weighted mean coefficient	weighted mean standard error	significance
(Intercept)		100	39.09	16.36	*	100	45.17	22.48	*
habitat and resource use	(i) breadth of habitat use	100	1.38	0.48	**	100	1.95	0.64	**
	(ii) vegetation structure:	45				45			
	short vs. medium		-0.25	0.38	n.s.		-0.35	0.53	n.s.
	short vs. tall		0.49	0.55	n.s.		0.56	0.73	n.s.
	medium vs. tall		0.74	0.44	n.s.		0.91	0.57	n.s.
	(iii) oviposition site:	100				100			
	vegetation vs. ground		1.07	0.38	**		1.47	0.51	**
	vegetation vs. ground or vegetation		0.98	0.42	*		1.35	0.58	*
	ground vs. ground or vegetation		-0.09	0.29	n.s.		-0.12	0.39	n.s.
	(iv) diet:	21				26			
	herbivorous vs. not herbivorous		-0.08	0.35	n.s.		-0.18	0.47	n.s.
life history	(v) mean body size	26	-0.50	1.29	n.s.	26	-0.26	1.78	n.s.
	(vi) generations per year:	11				9			
	one vs. half		-0.32	0.48	n.s.		-0.45	0.64	n.s.
	one vs. half or one		-0.21	0.67	n.s.		-0.25	0.88	n.s.
	half vs. half or one		0.12	0.62	n.s.		0.20	0.82	n.s.
	(vii) winter stage:	28				30			
	egg vs. not egg		0.01	0.63	n.s.		0.13	0.91	n.s.
	(viii) phenology	30	-0.17	0.21	n.s.	38	-0.26	0.29	n.s.
dispersal ability	(ix) wing morph:	21				19			
	short vs. long		0.12	0.78	n.s.		0.22	1.06	n.s.
	short vs. dimorphic		-0.14	0.92	n.s.		-0.18	1.19	n.s.
	long vs. dimorphic		-0.27	0.42	n.s.		-0.40	0.53	n.s.
	(x) wing load	40	0.32	0.32	n.s.	38	0.39	0.46	n.s.
distribution	(xi) average latitude	100	-0.76	0.32	*	98	-0.90	0.43	*

Summary of results for sets of top PGLS models with ΔAIC<4 (47 models for “uncorrected range change”, and 53 models for “corrected range change”). The importance of traits is indicated by the frequency with which they are included in the top model set (% included), and by their weighted mean coefficients, standard errors and significance levels. Significance levels: *= p<0.05, **=p<0.01. Results given are for minimum adequate recording effort, i.e. for “surveyed squares” with a minimum of 1 species recorded in both 1980-9 and 2000-9.

S 3.6 Table. Amount of overall variation explained by models.

		“uncorrected range change”				“corrected range change”			
		level of recording effort (minimum number of species recorded in “surveyed squares”)				level of recording effort (minimum number of species recorded in “surveyed squares”)			
		1	2	3	4	1	2	3	4
all species	minimum	0.033	0.033	0.038	0.032	0.029	0.031	0.033	0.030
	weighted mean	0.543	0.515	0.495	0.506	0.558	0.530	0.519	0.525
	maximum	0.590	0.569	0.554	0.563	0.607	0.586	0.578	0.582
species excluding *C. discolor* and *M. roeselii*	minimum	0.000	0.002	0.004	0.000	0.000	0.001	0.007	0.032
	weighted mean	0.118	0.126	0.131	0.129	0.116	0.130	0.137	0.167
	maximum	0.241	0.192	0.194	0.196	0.237	0.189	0.198	0.242

Minima, weighted means and maxima of adjusted deviance (D^2) for top sets of GLM models for two range change measures and four levels of recording effort.

S 3.7 Table. Impacts of species traits on distribution changes of British grasshoppers and crickets (excluding Conocephalus discolor and Metrioptera roeselii) between the 1980s and 2000s, phylogenetic models.

		"uncorrected range change"				"corrected range change"			
	trait	% included	weighted mean coefficient	weighted mean standard error	significance	% included	weighted mean coefficient	weighted mean standard error	significance
(Intercept)		100	0.98	3.12	n.s.	100	3.71	8.94	n.s.
habitat and resource use	(i) breadth of habitat use	50	0.38	0.30	n.s.	47	0.97	0.88	n.s.
	(ii) vegetation structure:	3				5			
	short vs. medium		-0.13	0.24	n.s.		-0.31	0.73	n.s.
	short vs. tall		-0.01	0.30	n.s.		0.16	0.93	n.s.
	medium vs. tall		0.12	0.25	n.s.		0.46	0.71	n.s.
	(iii) oviposition site:	24				22			
	vegetation vs. ground		0.24	0.24	n.s.		0.56	0.73	n.s.
	vegetation vs. ground or vegetation		0.04	0.26	n.s.		-0.01	0.79	n.s.
	ground vs. ground or vegetation		-0.20	0.18	n.s.		-0.57	0.51	n.s.
	(iv) diet:	20				18			
	herbivorous vs. not herbivorous		-0.03	0.19	n.s.		-0.06	0.53	n.s.
life history	(v) mean body size	59	-1.06	0.72	n.s.	67	-3.24	2.08	n.s.
	(vi) generations per year:	2				4			
	one vs. half		0.02	0.24	n.s.		0.17	0.70	n.s.
	one vs. half or one		0.04	0.27	n.s.		0.29	0.80	n.s.
	half vs. half or one		0.02	0.34	n.s.		0.12	0.94	n.s.
	(vii) winter stage:	32				33			
	egg vs. not egg		-0.21	0.36	n.s.		-0.68	1.04	n.s.
	(viii) phenology	38	0.12	0.11	n.s.	42	0.38	0.31	n.s.
dispersal ability	(ix) wing morph:	15				8			
	short vs. long		0.18	0.28	n.s.		0.43	0.74	n.s.
	short vs. dimorphic		-0.07	0.31	n.s.		-0.17	0.77	n.s.
	long vs. dimorphic		-0.25	0.20	n.s.		-0.60	0.58	n.s.
	(x) wing load	18	-0.03	0.17	n.s.	18	-0.05	0.45	n.s.
distribution	(xi) average latitude	25	-0.05	0.23	n.s.	24	-0.21	0.64	n.s.

Summary of results for sets of top PGLS models with ΔAIC<4 (95 models for "uncorrected range change", and 79 models for "corrected range change"). The importance of traits is indicated by the frequency with which they are included in the top model set (% included), and by their weighted mean coefficients, standard errors and significance levels. Results given are for minimum adequate recording effort, i.e. for "surveyed squares" with a minimum of 1 species recorded in both 1980-9 and 2000-9.

S 3.8 Table. Fitted range change values.

	all species								species excluding *C. discolor* and *M. roeselii*							
	"uncorrected range change" recording effort level				"corrected range change" recording effort level				"uncorrected range change" recording effort level				"corrected range change" recording effort level			
Species	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
M. thalassinum	0.33±0.24	0.29±0.25	0.25±0.27	0.32±0.25	0.25±0.29	0.2±0.3	0.2±0.31	0.27±0.3	0.08±0.09	0.05±0.08	0.03±0.08	0.04±0.11	0.21±0.23	0.16±0.21	0.1±0.2	0.14±0.32
T. viridissima	-0.04±0.09	-0.04±0.09	-0.04±0.1	-0.05±0.08	-0.42±0.12	-0.42±0.12	-0.42±0.13	-0.42±0.1	-0.22±0.13	-0.26±0.13	-0.28±0.13	-0.31±0.13	-0.71±0.39	-0.82±0.35	-0.8±0.35	-0.93±0.35
P. griseoaptera	0.48±0.15	0.54±0.16	0.53±0.17	0.66±0.16	0.49±0.2	0.57±0.21	0.61±0.21	0.74±0.19	0.07±0.07	0.06±0.07	0.03±0.08	0.13±0.12	0.1±0.18	0.06±0.17	0.07±0.2	0.3±0.31
P. albopunctata	0.08±0.05	0.06±0.05	0.08±0.05	0.04±0.05	-0.34±0.09	-0.36±0.1	-0.38±0.09	-0.4±0.07	-0.08±0.06	-0.09±0.04	-0.1±0.04	-0.1±0.05	-0.22±0.17	-0.25±0.12	-0.26±0.1	-0.28±0.11
M. brachyptera	-0.03±0.13	-0.01±0.14	-0.03±0.15	0±0.15	-0.35±0.18	-0.34±0.2	-0.38±0.2	-0.36±0.18	-0.01±0.13	0.04±0.09	0.02±0.08	0.05±0.09	-0.03±0.31	0.1±0.22	0.06±0.22	0.14±0.23
M. roeselii	1.11±0.14	1.11±0.15	1.08±0.16	1.1±0.16	1.26±0.2	1.22±0.2	1.17±0.2	1.16±0.19	-	-	-	-	-	-	-	-
C. discolor	1.93±0.08	1.96±0.09	1.99±0.11	2.01±0.1	2.26±0.12	2.25±0.17	2.22±0.17	2.23±0.16	-	-	-	-	-	-	-	-
C. dorsalis	1.16±0.1	1.15±0.12	1.14±0.12	1.14±0.12	1.28±0.14	1.22±0.16	1.17±0.15	1.16±0.15	0.16±0.11	0.11±0.08	0.07±0.08	0.09±0.09	0.38±0.31	0.26±0.24	0.19±0.22	0.26±0.27
L. punctatissima	0.35±0.15	0.4±0.15	0.41±0.16	0.55±0.15	0.27±0.2	0.34±0.2	0.39±0.2	0.55±0.17	0.14±0.09	0.15±0.09	0.13±0.1	0.26±0.12	0.35±0.25	0.38±0.24	0.36±0.26	0.71±0.32
N. sylvestris	-0.41±0.15	-0.35±0.16	-0.31±0.19	-0.29±0.17	-0.91±0.2	-0.81±0.21	-0.76±0.22	-0.7±0.2	0.14±0.13	0.23±0.1	0.26±0.09	0.29±0.1	0.52±0.33	0.73±0.28	0.77±0.25	0.88±0.23
T. ceperoi	0.57±0.09	0.57±0.09	0.61±0.13	0.56±0.08	0.36±0.12	0.35±0.13	0.35±0.16	0.32±0.12	0.17±0.1	0.17±0.11	0.2±0.1	0.15±0.11	0.53±0.25	0.55±0.24	0.59±0.23	0.47±0.28
T. subulata	0.3±0.08	0.29±0.08	0.32±0.11	0.24±0.08	0.15±0.1	0.12±0.11	0.16±0.12	0.05±0.11	0.15±0.06	0.16±0.06	0.17±0.06	0.12±0.06	0.37±0.18	0.4±0.17	0.47±0.15	0.29±0.16
T. undulata	0.31±0.08	0.29±0.09	0.3±0.11	0.22±0.1	0.2±0.11	0.18±0.13	0.21±0.14	0.09±0.13	0.18±0.07	0.19±0.07	0.2±0.06	0.14±0.07	0.43±0.2	0.48±0.2	0.56±0.16	0.36±0.19
S. grossum	-0.18±0.06	-0.22±0.08	-0.19±0.08	-0.22±0.09	-0.66±0.09	-0.72±0.13	-0.7±0.12	-0.72±0.12	-0.15±0.1	-0.19±0.09	-0.19±0.09	-0.19±0.08	-0.45±0.27	-0.57±0.25	-0.55±0.24	-0.56±0.21
S. lineatus	-0.12±0.1	-0.13±0.11	-0.12±0.11	-0.13±0.11	-0.46±0.14	-0.44±0.17	-0.42±0.15	-0.44±0.14	-0.09±0.07	-0.11±0.05	-0.12±0.05	-0.12±0.05	-0.33±0.21	-0.36±0.17	-0.34±0.14	-0.4±0.15
O. rufipes	-0.61±0.13	-0.53±0.16	-0.53±0.16	-0.46±0.17	-1.24±0.2	-1.1±0.23	-1.12±0.22	-1.01±0.23	-0.19±0.15	-0.09±0.09	-0.08±0.07	-0.07±0.06	-0.48±0.42	-0.21±0.21	-0.22±0.2	-0.2±0.17
O. viridulus	-0.25±0.09	-0.32±0.08	-0.39±0.08	-0.42±0.08	-0.49±0.14	-0.56±0.14	-0.57±0.13	-0.67±0.12	-0.03±0.07	-0.06±0.05	-0.09±0.05	-0.1±0.05	-0.21±0.2	-0.27±0.16	-0.26±0.15	-0.35±0.17
C. brunneus	-0.28±0.07	-0.26±0.07	-0.3±0.06	-0.28±0.07	-0.56±0.09	-0.51±0.1	-0.51±0.1	-0.49±0.1	-0.09±0.08	-0.09±0.06	-0.12±0.06	-0.13±0.06	-0.36±0.22	-0.34±0.17	-0.34±0.16	-0.43±0.16
C. vagans	0.14±0.05	0.17±0.06	0.19±0.06	0.21±0.06	-0.25±0.08	-0.21±0.09	-0.22±0.09	-0.16±0.08	-0.05±0.06	-0.04±0.05	-0.04±0.05	-0.03±0.06	-0.1±0.18	-0.07±0.13	-0.11±0.13	-0.04±0.17
C. parallelus	0.42±0.08	0.42±0.09	0.4±0.15	0.37±0.08	0.37±0.12	0.37±0.12	0.36±0.17	0.3±0.11	0.03±0.11	-0.01±0.1	-0.05±0.09	-0.05±0.09	-0.09±0.27	-0.17±0.2	-0.17±0.2	-0.23±0.22
C. albomarginatus	-0.07±0.07	-0.15±0.08	-0.17±0.08	-0.23±0.09	-0.36±0.1	-0.46±0.13	-0.47±0.13	-0.56±0.14	0.02±0.06	-0.03±0.04	-0.05±0.04	-0.05±0.04	-0.01±0.18	-0.12±0.1	-0.14±0.1	-0.13±0.11
G. rufus	0.04±0.08	0.02±0.1	0.02±0.11	0.01±0.12	-0.3±0.13	-0.34±0.18	-0.34±0.17	-0.33±0.18	-0.02±0.09	-0.05±0.06	-0.06±0.05	-0.05±0.07	-0.06±0.26	-0.14±0.16	-0.18±0.15	-0.12±0.19
M. maculatus	-0.44±0.06	-0.44±0.06	-0.5±0.06	-0.49±0.06	-0.76±0.09	-0.74±0.1	-0.74±0.1	-0.75±0.1	-0.01±0.08	0.01±0.07	-0.01±0.07	-0.01±0.07	-0.07±0.22	0.02±0.17	-0.01±0.19	-0.05±0.18

Weighted means ± weighted standard deviations across sets of top GLM models with ΔAIC<4 (weightings by Akaike weights). Results for four levels of recording effort, "uncorrected" and "corrected range change", and for models with all species and models excluding *C. discolor* and *M. roeselii*

Appendix to Chapter 4

S 4.1 Table. Data for analysis of weather effects on annual colonisation rate

	Conocephalus discolor						*Metrioptera roeselii*						warmth (GDD10)				rainfall (mm)			
	no. hectads occupied	no. hectads in typical max. dispersal distance	no. hectads surveyed in typical max. dispersal distance	no. hectads colonised	no. surveyed hectads in typical max. dispersal distance colonised	proportion of surveyed hectads in typical max. dispersal distance colonised	no. hectads occupied	no. hectads in typical max. dispersal distance	no. hectads surveyed in typical max. dispersal distance	no. hectads colonised	no. surveyed hectads in typical max. dispersal distance colonised	proportion of surveyed hectads in typical max. dispersal distance colonised	April-July		August-October		April-July		August-October	
year													same year	prev. year	same year	prev. year	same year	prev. year	same year	prev. year
1977	22	96	25	2	2	0.080	58	217	42	3	3	0.071	371	638	358	408	161	92	157	255
1978	24	97	16	1	1	0.063	61	225	39	0	0	0.000	368	371	376	358	227	161	89	157
1979	25	96	19	1	1	0.053	61	225	30	3	2	0.067	425	368	370	376	217	227	144	89
1980	26	95	11	0	0	0.000	64	237	32	0	0	0.000	406	425	386	370	208	217	209	144
1981	26	95	13	1	1	0.077	64	237	30	0	0	0.000	398	406	376	386	218	208	225	209
1982	27	94	30	3	3	0.100	64	237	55	6	6	0.109	532	398	388	376	195	218	232	225
1983	30	96	35	6	6	0.171	70	242	64	0	0	0.000	503	532	414	388	258	195	135	232
1984	36	93	28	6	6	0.214	70	242	77	18	18	0.234	450	503	426	414	144	258	199	135
1985	42	107	39	4	4	0.103	88	241	82	3	3	0.037	420	450	370	426	258	144	119	199
1986	46	103	20	1	1	0.050	91	238	64	0	0	0.000	429	420	305	370	205	258	191	119
1987	47	102	26	1	1	0.038	91	238	55	0	0	0.000	435	429	365	305	261	205	254	191
1988	48	104	33	1	1	0.030	91	238	56	1	1	0.018	409	435	355	365	216	261	152	254
1989	49	103	27	6	6	0.222	92	238	82	5	5	0.061	552	409	466	355	184	216	128	152
1990	55	118	61	17	10	0.164	97	236	91	11	10	0.110	521	552	480	466	120	184	138	128
1991	72	219	91	24	23	0.253	108	258	100	15	13	0.130	429	521	443	480	216	120	112	138
1992	96	223	84	12	11	0.131	123	279	78	6	6	0.077	562	429	320	443	228	216	252	112
1993	108	273	105	4	3	0.029	129	277	81	6	6	0.074	467	562	276	320	256	228	242	252
1994	112	288	125	25	23	0.184	135	273	79	14	14	0.177	513	467	360	276	180	256	225	242
1995	137	365	150	28	28	0.187	149	271	80	6	6	0.075	567	513	508	360	96	180	140	225
1996	165	386	179	25	25	0.140	155	273	101	25	20	0.198	453	567	399	508	113	96	140	140
1997	190	384	180	38	36	0.200	180	332	129	20	17	0.132	484	453	486	399	230	113	150	140
1998	228	386	154	14	14	0.091	200	371	116	24	23	0.198	438	484	386	486	267	230	235	150
1999	242	378	181	30	30	0.166	224	361	132	30	27	0.205	525	438	434	386	194	267	255	235
2000	272	406	159	16	15	0.094	254	410	123	20	17	0.138	424	525	415	434	289	194	287	255
2001	288	417	125	22	21	0.168	274	420	101	9	9	0.089	491	424	428	415	226	289	252	287
2002	310	460	120	14	14	0.117	283	419	81	3	3	0.037	468	491	402	428	234	226	182	252
2003	324	446	163	38	38	0.233	286	416	121	17	17	0.140	581	468	452	402	199	234	77	182
2004	362	464	136	25	24	0.176	303	425	117	15	15	0.128	499	581	432	452	225	199	269	77
2005	387	468	97	11	11	0.113	318	426	95	16	16	0.168	503	499	450	432	182	225	191	269
2006	398	470	154	44	43	0.279	334	431	125	38	37	0.296	611	503	489	450	186	182	240	191
2007	442	478	134	56	54	0.403	372	439	121	55	54	0.446	504	611	372	489	345	186	125	240
2008	498	478	91	16	16	0.176	427	426	80	14	14	0.175	485	504	356	372	238	345	216	125
2009	514	482	86	27	26	0.302	441	418	72	19	18	0.250	512	485	426	356	212	238	116	216
2010	541	498	126	17	17	0.135	460	428	119	22	22	0.185	550	512	354	426	114	212	229	116
2011	558	499	114	9	8	0.070	482	420	94	13	12	0.128	520	550	431	354	148	114	127	229
2012	567	512	57	14	14	0.246	495	425	54	18	18	0.333	390	520	366	431	403	148	208	127

For definitions of parameters see Methods. The proportions of surveyed hectads in the typical maximum dispersal distance that were colonised (grey shading) were used as measure of annual colonisation rate (response variable).

S 4.2 Table. Field observations of incidence of long-wingedness (macroptery) for *Conocephalus discolor*, and associated site, field visit, population and seasonal weather parameters

(table continued on next page)

site		field visit						population					seasonal weather							
													warmth (GDD10)				rainfall (mm)			
													April-July		August-October		April-July		August-October	
site name	grid reference	date	day of year	start time	end time	time of day	mean temperature	no. short-winged	no. long-winged	population density	distance from core	age of population	same year	prev. year	same year	prev. year	same year	prev. year	same year	prev. year
Alby Hill	TG1833	22/09/08	266	15:00	18:00	0.80	13.27	9	0	0.050	238	2	481	479	381	392	186	389	270	171
Alby Hill	TG1833	10/09/09	253	12:15	15:15	0.57	13.14	33	1	0.189	238	3	498	481	460	381	210	186	91	270
Alby Hill	TG1833	04/09/10	247	10:00	12:30	0.38	13.58	29	2	0.207	238	4	552	498	382	460	148	210	256	91
Alby Hill	TG1833	22/09/11	265	09:45	11:35	0.33	13.14	34	0	0.309	238	5	521	552	470	382	142	148	136	256
Alby Hill	TG1833	09/09/12	253	10:30	12:50	0.41	19.20	31	0	0.221	238	6	397	521	392	470	299	142	181	136
Bovey Heath	SX8276	27/08/08	240	14:30	18:30	0.74	16.40	10	5	0.063	103	11	498	516	372	417	445	380	324	161
Bovey Heath	SX8276	01/09/09	244	13:40	17:00	0.66	14.96	12	5	0.085	103	12	500	498	427	372	324	445	200	324
Bovey Heath	SX8276	12/09/10	255	12:45	16:00	0.59	14.26	17	4	0.108	103	13	529	500	392	427	186	324	288	200
Bovey Heath	SX8276	29/09/11	272	10:30	13:05	0.39	18.33	28	2	0.194	103	14	515	529	445	392	140	186	225	288
Bovey Tracey	SX8178	01/09/09	244	18:00	19:30	0.91	14.83	21	1	0.244	104	12	490	487	417	363	326	454	211	350
Bovey Tracey	SX8178	12/09/10	255	16:15	17:45	0.80	14.15	35	0	0.389	104	13	518	490	383	417	195	326	302	211
Bovey Tracey	SX8178	29/09/11	272	13:50	15:10	0.62	18.22	46	0	0.575	104	14	505	518	436	383	151	195	231	302
Broadwell	SP4666	18/09/08	262	15:00	17:10	0.75	12.53	17	3	0.308	150	2	512	519	364	387	233	380	248	104
Broadwell	SP4666	19/08/09	231	18:00	21:00	0.94	19.77	3	1	0.044	150	3	539	512	422	364	226	233	108	248
Broadwell	SP4666	22/09/10	265	11:00	14:30	0.48	15.62	18	2	0.190	150	4	583	539	367	422	114	226	208	108
Broadwell	SP4666	28/09/11	271	10:40	16:30	0.56	18.10	15	0	0.086	150	5	545	583	450	367	118	114	101	208
Broadwell	SP4666	06/09/12	250	12:20	16:50	0.61	13.76	11	0	0.081	150	6	421	545	368	450	408	118	183	101
Dawlish Warren	SX9879	27/08/08	240	09:45	12:30	0.35	16.59	18	0	0.109	87	11	517	537	383	428	374	269	238	134
Dawlish Warren	SX9879	01/09/09	244	10:00	12:00	0.34	15.17	22	1	0.192	87	12	519	517	440	383	283	374	154	238
Dawlish Warren	SX9879	12/09/10	255	09:00	11:15	0.26	14.37	30	1	0.230	87	13	552	519	404	440	124	283	210	154
Dawlish Warren	SX9879	30/09/11	273	09:00	10:40	0.22	18.53	19	0	0.190	87	14	534	552	459	404	110	124	179	210
Dawlish Warren	SX9879	19/10/12	293	09:25	10:50	0.23	10.72	1	0	0.012	87	15	429	534	401	459	442	110	339	179

site		field visit						population					seasonal weather							
site name	grid reference	date	day of year	start time	end time	time of day	mean temperature	no. short-winged	no. long-winged	population density	distance from core	age of population	warmth (GDD10)				rainfall (mm)			
													April-July		August-October		April-July		August-October	
													same year	prev. year	same year	prev. year	same year	prev. year	same year	prev. year
Drakelow	SK2220	27/09/08	271	13:00	17:30	0.70	11.68	35	2	0.137	212	2	498	506	361	385	193	358	240	94
Drakelow	SK2220	20/09/09	263	15:30	17:30	0.79	13.53	32	0	0.267	212	3	528	498	412	361	310	193	107	240
Drakelow	SK2220	02/09/10	245	14:25	16:45	0.68	14.72	34	1	0.250	212	4	569	528	361	412	115	310	221	107
Drakelow	SK2220	26/09/11	269	10:45	13:00	0.41	14.89	17	0	0.126	212	5	530	569	435	361	137	115	105	221
Drakelow	SK2220	07/09/12	251	16:40	18:05	0.83	16.76	16	0	0.188	212	6	408	530	357	435	389	137	184	105
Earlham	TG1910	21/09/08	265	11:00	16:00	0.56	13.13	13	7	0.067	209	0	507	506	392	406	197	371	226	184
Earlham	TG1910	09/09/09	252	12:30	16:30	0.63	14.97	30	12	0.175	209	1	525	507	477	392	204	197	78	226
Earlham	TG1910	04/09/10	247	14:40	17:15	0.73	13.96	23	2	0.161	209	2	576	525	396	477	122	204	259	78
Earlham	TG1910	22/09/11	265	14:20	16:30	0.72	13.58	22	0	0.169	209	3	544	576	491	396	136	122	132	259
Earlham	TG1910	09/09/12	253	15:40	17:30	0.78	19.41	58	0	0.527	209	4	418	544	408	491	371	136	187	132
Little Wittenham	SU5692	18/08/09	230	16:00	18:00	0.77	16.86	30	0	0.250	80	14	543	524	428	365	190	280	114	192
Little Wittenham	SU5692	01/09/10	244	13:40	14:40	0.58	14.03	2	0	0.033	80	15	589	543	376	428	91	190	200	114
Otmoor	SP5612	08/09/08	252	11:00	16:30	0.55	14.26	19	2	0.127	108	10	532	541	374	397	269	315	186	127
Otmoor	SP5612	16/08/09	228	14:30	17:30	0.70	17.41	26	2	0.156	108	11	553	532	436	374	222	269	107	186
Otmoor	SP5612	31/08/10	243	16:40	18:40	0.84	12.94	20	0	0.333	108	12	601	553	383	436	108	222	205	107
Otmoor	SP5612	02/09/11	245	16:00	18:00	0.79	17.12	41	0	0.342	108	13	561	601	466	383	141	108	110	205
Otmoor	SP5612	05/09/12	249	16:15	19:15	0.85	13.73	19	0	0.211	108	14	439	561	383	466	406	141	234	110
St Ives	TL3270	11/08/08	224	12:30	16:30	0.60	16.61	13	2	0.125	163	9	556	562	400	420	177	260	162	140
St Ives	TL3270	08/09/09	251	14:00	16:00	0.66	20.61	14	1	0.250	163	10	584	556	475	400	166	177	109	162
St Ives	TL3270	03/09/10	246	15:10	18:50	0.80	14.45	21	1	0.200	163	11	638	584	404	475	103	166	231	109
St Ives	TL3270	23/09/11	266	09:55	16:00	0.51	13.42	18	2	0.110	163	12	595	638	503	404	110	103	100	231
St Ives	TL3270	08/09/12	252	11:05	14:40	0.50	17.41	25	0	0.233	163	13	464	595	411	503	343	110	159	100
Swaffham Prior	TL5466	10/08/08	223	17:00	20:40	0.88	17.95	3	1	0.036	158	9	562	566	406	426	205	260	173	132
Swaffham Prior	TL5466	06/09/09	249	13:30	17:30	0.69	15.32	29	1	0.250	158	10	587	562	486	406	156	205	100	173

Table continued from previous page. For definitions of parameters see section 4.3. A matrix of the numbers of short-winged (brachypterous) and long-winged (macropterous) individuals (grey shading) was used as response variable in the analysis of weather effects on incidence of long-wingedness.

S 4.3 Table. Field observations of incidence of long-wingedness (macroptery) for *Metrioptera roeselii*, and associated site, field visit, population and seasonal weather parameters

site		field visit						population					seasonal weather							
site name	grid reference	date	day of year	start time	end time	time of day	mean temperature	no. short-winged	no. long-winged	population density	distance from core	age of population	warmth (GDD10)				rainfall (mm)			
													April-July		August-October		April-July		August-October	
													same year	prev. year	same year	prev. year	same year	prev. year	same year	prev. year
Alby Hill	TG1833	22/09/11	265	11:45	12:15	0.44	13.14	7	1	0.267	100	3	521	552	470	382	142	148	136	256
Broadwell	SP4666	18/09/08	262	15:00	17:10	0.75	12.53	1	0	0.015	122	2	512	519	364	387	233	380	248	104
Broadwell	SP4666	19/08/09	231	18:00	21:00	0.94	19.77	12	2	0.156	122	3	539	512	422	364	226	233	108	248
Broadwell	SP4666	22/09/10	265	11:00	14:30	0.48	15.62	23	1	0.229	122	4	583	539	367	422	114	226	208	108
Broadwell	SP4666	28/09/11	271	10:40	16:30	0.56	18.10	24	5	0.166	122	5	545	583	450	367	118	114	101	208
Broadwell	SP4666	06/09/12	250	12:20	16:50	0.61	13.76	30	0	0.222	122	6	421	545	368	450	408	118	183	101
Little Wittenham	SU5692	10/09/08	254	10:00	11:30	0.33	15.69	50	0	0.556	68	18	524	532	365	388	280	342	192	108
Little Wittenham	SU5692	18/08/09	230	13:00	14:30	0.54	16.86	55	4	0.656	68	19	543	524	428	365	190	280	114	192
Little Wittenham	SU5692	01/09/10	244	12:00	13:30	0.48	14.03	23	2	0.278	68	20	589	543	376	428	91	190	200	114
Little Wittenham	SU5692	02/08/11	214	10:50	12:50	0.41	20.11	28	6	0.283	68	21	550	589	456	376	126	91	119	200
Little Wittenham	SU5692	05/09/12	249	12:35	14:15	0.53	13.74	49	1	0.500	68	22	430	550	377	456	362	126	199	119
Otmoor	SP5612	08/09/08	252	11:00	16:30	0.55	14.26	19	1	0.121	70	10	532	541	374	397	269	315	186	127
Otmoor	SP5612	24/07/09	205	14:00	16:30	0.63	15.15	20	0	0.133	70	11	553	532	436	374	222	269	107	186
Otmoor	SP5612	31/08/10	243	16:40	18:40	0.84	12.94	18	2	0.333	70	12	601	553	383	436	108	222	205	107
Otmoor	SP5612	31/07/11	212	14:00	15:45	0.61	17.91	18	4	0.419	70	13	561	601	466	383	141	108	110	205
Otmoor	SP5612	08/08/12	221	16:25	18:25	0.78	17.49	24	0	0.400	70	14	439	561	383	466	406	141	234	110
St Ives	TL3270	11/08/08	224	12:30	16:30	0.60	16.61	24	0	0.200	75	10	556	562	400	420	177	260	162	140
St Ives	TL3270	08/09/09	251	14:00	16:00	0.66	20.61	46	3	0.817	75	11	584	556	475	400	166	177	109	162
St Ives	TL3270	03/09/10	246	15:10	18:50	0.80	14.45	20	1	0.191	75	12	638	584	404	475	103	166	231	109
St Ives	TL3270	23/09/11	266	09:55	16:00	0.51	13.42	43	0	0.236	75	13	595	638	503	404	110	103	100	231
St Ives	TL3270	08/09/12	252	11:05	14:40	0.50	17.41	50	1	0.474	75	14	464	595	411	503	343	110	159	100
Swaffham Prior	TL5466	10/08/08	223	17:00	20:40	0.88	17.95	4	0	0.036	51	12	562	566	406	426	205	260	173	132
Swaffham Prior	TL5466	06/09/09	249	13:30	17:30	0.69	15.32	11	0	0.092	51	13	587	562	486	406	156	205	100	173

For definitions of parameters see section 4.3. A matrix of the numbers of short-winged (brachypterous) and long-winged (macropterous) individuals (grey shading) was used as response variable in the analysis of weather effects on incidence of long-wingedness.

S 4.4a Table. Modelled correlations between predictive variables in the analysis of weather effects on incidence of long-wingedness for *Conocephalus discolor*

			warmth (GDD10)			rainfall (mm)					day of year	time of day	mean temperature	population density	distance from core
			April-July	August-October		April-July			August-October						
			previous year	same year	previous year	same year	same year, squared	previous year	same year	previous year					
warmth (GDD10)	April-July	same year	-0.18 +-0.04 (n=23)	0.00 +-0.05 (n=15)	-0.21 +-0.23 (n=3)	0.58 +-0.03 (n=8)	-	0.18 +-0.02 (n=33)	-0.15 +-0.04 (n=14)	0.19 +-0.03 (n=7)	0.53 +-0.20 (n=2)	-0.07 +-0.02 (n=3)	0.03 +-0.03 (n=2)	-0.15 +-0.02 (n=35)	0.19 +-0.06 (n=6)
		previous year		-0.13 +-0.01 (n=17)	0.02 +-0.02 (n=4)	-0.02 +-0.05 (n=6)	-	0.44 +-0.01 (n=29)	-0.10 +-0.02 (n=10)	0.16 +-0.02 (n=10)	-0.08 +-0.06 (n=3)	0.12 +-0.01 (n=3)	0.08 +-0.02 (n=3)	0.18 +-0.01 (n=31)	0.19 +-0.06 (n=3)
	August-October	same year			0.50 +-0.15 (n=3)	0.02 +-0.03 (n=3)	-	0.46 +-0.03 (n=31)	0.73 +-0.06 (n=4)	-0.68 +-0.04 (n=21)	0.11 +-0.07 (n=3)	-0.18 +-0.04 (n=4)	-0.14 +-0.07 (n=3)	-0.15 +-0.02 (n=31)	0.04 +-0.08 (n=5)
		previous year				-	-	0.38 +-0.11 (n=5)	-0.84 +-0.00 (n=1)	0.32 +-0.01 (n=2)	-	-	-	-0.11 +-0.06 (n=5)	-
rainfall (mm)	April-July	same year					-	-0.18 +-0.03 (n=9)	0.19 +-0.05 (n=2)	-0.02 +-0.04 (n=2)	-	-	-	0.09 +-0.02 (n=10)	0.30 +-0.00 (n=1)
		same year, squared						-	-	-	-	-	-	-	-
		previous year							-0.38 +-0.04 (n=17)	-0.42 +-0.03 (n=24)	0.16 +-0.03 (n=4)	-0.29 +-0.03 (n=5)	0.14 +-0.07 (n=4)	0.19 +-0.02 (n=50)	0.26 +-0.04 (n=8)
	August-October	same year								0.47 +-0.13 (n=6)	-0.29 +-0.00 (n=1)	0.07 +-0.00 (n=1)	0.29 +-0.00 (n=1)	0.01 +-0.03 (n=17)	-0.11 +-0.00 (n=2)
		previous year									-0.12 +-0.00 (n=2)	0.24 +-0.01 (n=3)	0.01 +-0.01 (n=2)	0.10 +-0.02 (n=24)	0.15 +-0.08 (n=3)
day of year												-	-	-0.09 +-0.04 (n=4)	-
time of day													-	-0.10 +-0.02 (n=5)	-
mean temperature														0.04 +-0.02 (n=4)	-
population density															0.13 +-0.03 (n=8)

Means and standard errors of correlations between fixed effects estimated in the set of 52 top GLMM models with ΔAIC < 4 for *Conocephalus discolor*. Numbers in brackets indicate the number of top models in which the respective combination of variables occurred. Mean correlation values of >= 0.70 or <=-0.70 are shaded grey. Combinations of variables which did not occur in top models are marked by a hyphen.

S 4.4b Table. Modelled correlations between predictive variables in the analysis of weather effects on incidence of long-wingedness for *Metrioptera roeselii*

			warmth (GDD10)			**rainfall (mm)**					**day of year**	**time of day**	**mean temperature**	**population density**	**distance from core**
			April-July	**August-October**		**April-July**			**August-October**						
			previous year	**same year**	**previous year**	**same year**	**same year, squared**	**previous year**	**same year**	**previous year**					
warmth (GDD10)	**April-July**	**same year**	-0.07 +-0.06 (n=21)	-0.09 +-0.05 (n=18)	-0.41 +-0.03 (n=13)	0.73 +-0.03 (n=106)	0.17 +-0.05 (n=21)	-0.51 +-0.03 (n=20)	-0.24 +-0.05 (n=14)	0.47 +-0.03 (n=11)	0.14 +-0.03 (n=28)	-0.61 +-0.01 (n=86)	0.03 +-0.02 (n=73)	-0.52 +-0.02 (n=27)	0.55 +-0.02 (n=13)
		previous year		-0.21 +-0.04 (n=12)	-0.21 +-0.06 (n=8)	0.10 +-0.03 (n=46)	0.01 +-0.03 (n=24)	0.69 +-0.03 (n=34)	0.02 +-0.11 (n=4)	0.12 +-0.11 (n=4)	0.06 +-0.03 (n=6)	0.16 +-0.02 (n=17)	-0.03 +-0.06 (n=17)	0.17 +-0.05 (n=4)	0.29 +-0.04 (n=3)
	August-October	**same year**			0.07 +-0.13 (n=8)	-0.32 +-0.07 (n=44)	0.68 +-0.04 (n=26)	0.70 +-0.03 (n=32)	0.66 +-0.04 (n=6)	-0.64 +-0.08 (n=9)	-0.15 +-0.15 (n=3)	0.01 +-0.04 (n=18)	-0.37 +-0.07 (n=15)	-0.58 +-0.05 (n=12)	0.16 +-0.04 (n=2)
		previous year				-0.14 +-0.08 (n=26)	-0.41 +-0.07 (n=9)	-0.04 +-0.07 (n=13)	-0.69 +-0.02 (n=3)	0.70 +-0.00 (n=1)	-0.23 +-0.05 (n=4)	0.05 +-0.05 (n=15)	0.42 +-0.05 (n=10)	0.03 +-0.17 (n=5)	0.13 +-0.00 (n=1)
rainfall (mm)	**April-July**	**same year**					-0.97 +-0.00 (n=52)	-0.48 +-0.05 (n=62)	0.02 +-0.09 (n=21)	0.06 +-0.10 (n=21)	0.23 +-0.03 (n=31)	-0.51 +-0.02 (n=93)	-0.08 +-0.02 (n=79)	-0.46 +-0.05 (n=37)	0.43 +-0.06 (n=15)
		same year, squared						0.67 +-0.03 (n=38)	-0.44 +-0.08 (n=8)	0.39 +-0.09 (n=6)	-0.33 +-0.05 (n=6)	0.07 +-0.02 (n=19)	0.38 +-0.06 (n=12)	0.01 +-0.09 (n=10)	0.04 +-0.07 (n=3)
		previous year							-0.21 +-0.08 (n=8)	-0.08 +-0.14 (n=10)	-0.11 +-0.06 (n=6)	-0.04 +-0.05 (n=18)	0.32 +-0.04 (n=15)	-0.44 +-0.07 (n=13)	0.14 +-0.14 (n=3)
	August-October	**same year**								0.82 +-0.00 (n=1)	-0.03 +-0.09 (n=3)	0.06 +-0.04 (n=14)	0.56 +-0.03 (n=12)	0.10 +-0.22 (n=3)	0.11 +-0.00 (n=1)
		previous year									0.11 +-0.04 (n=2)	-0.25 +-0.06 (n=11)	-0.25 +-0.06 (n=12)	0.44 +-0.17 (n=6)	-0.09 +-0.00 (n=1)
day of year												-0.12 +-0.02 (n=26)	0.34 +-0.02 (n=12)	-0.01 +-0.03 (n=11)	-0.72 +-0.02 (n=2)
time of day													0.00 +-0.01 (n=60)	0.36 +-0.01 (n=27)	-0.52 +-0.01 (n=12)
mean temperature														-0.29 +-0.03 (n=13)	-0.09 +-0.04 (n=12)
population density															0.28 +-0.08 (n=2)

Means and standard errors of correlations between fixed effects estimated in the set of 148 top GLMM models with ΔAIC < 4 for *Metrioptera roeselii*. Numbers in brackets indicate the number of top models in which the respective combination of variables occurred. Mean correlation values of >= 0.70 or <=-0.70 are shaded grey. The strong correlation between April-July rainfall and its square is to be expected.

S 4.5 Table. Comparison of colonisation metrics for different definitions of colonisation – with and without extinction.

		Conocephalus discolor		***Metrioptera roeselii***	
		without extinction	with extinction	without extinction	with extinction
Annual number of squares recorded as previously occupied	min	22	22	58	58
	max	567	501	495	468
	median	124.5	113.5	142	124
Annual number of squares gone extinct	min	-	0	-	0
	max	-	18	-	11
	median	-	3	-	2
	total 1977-2012	-	155	-	95
Annual number of surveyed squares colonised	min	0	0	0	0
	max	54	58	54	57
	median	12.5	14	11	13.5
	total 1977-2012	537	614	432	500
Annual proportion of surveyed squares colonised	min	0.00	0.00	0.00	0.00
	max	0.40	0.39	0.45	0.45
	mean ± SD	0.15 ± 0.09	0.15 ± 0.09	0.12 ± 0.10	0.14 ± 0.11
Maximum typical dispersal distance in km (95th percentile of dispersal distances)		31.6	31.6	28.8	28.3

Metrics of the annual numbers of 10x10km squares (hectads) recorded as occupied, gone extinct and colonised by *C. discolor* and *M. roeselii* in Britain between 1977 and 2012, and derived maximum typical dispersal distances. Results for two definitions of colonisation are compared: “without extinction” means that only the first record for each square was considered a colonisation and the square was assumed to remain occupied in all subsequent years. “With extinction” means that the focal species was assumed to go extinct in squares where it was not recorded in 4 years of visits, and any subsequent records were regarded as renewed colonisations.

S 4.6 Table. Ratios of residual deviance to degrees of freedom for sets of top models

	Analysis of weather effects on colonisation rate (GLMs)		**Analysis of weather effects on incidence of long-wingedness (GLMMs)**	
	Conocephalus discolor	*Metrioptera roeselii*	*Conocephalus discolor*	*Metrioptera roeselii*
min	1.84	3.75	2.78	2.91
max	1.99	4.19	2.89	3.28
mean	**1.94**	**3.94**	**2.85**	**3.17**

Minima, maxima and means of ratios of residual deviance to degrees of freedom for sets of top models with ΔAIC < 4.

S 4.7 Table. Effects of weather on annual colonisation rate of *Conocephalus discolor* and *Metrioptera roeselii*, assuming a reduced "maximum typical dispersal distance"

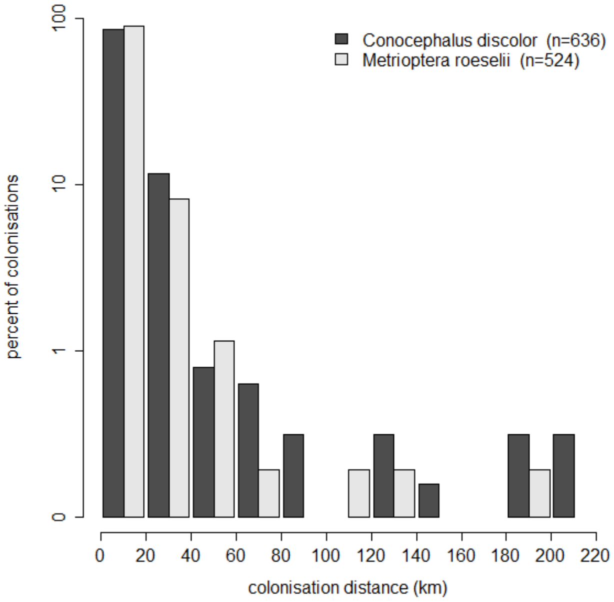
			Conocephalus discolor				***Metrioptera roeselii***			
			% included	**weighted mean coefficient**	**weighted mean standard error**	**sig**	**% included**	**weighted mean coefficient**	**weighted mean standard error**	**sig**
(Intercept)			100	-2.3676	6.0789		100	-78.2895	16.9080	
year			37	0.0038	0.0089		100	0.0402	0.0088	***
warmth (GDD10)	**April-July**	**same year**	100	-0.0025	0.0025		100	-0.0064	0.0030	*
		previous year	43	-0.0014	0.0014		39	-0.0009	0.0016	
	August-October	**same year**	100	0.0053	0.0014	***	94	0.0039	0.0015	*
		previous year	40	-0.0013	0.0014		56	0.0019	0.0015	
rainfall (mm)	**April-July**	**same year**	100	-0.0160	0.0058	**	100	-0.0294	0.0065	***
		same year, squared	100	-2.31E-05	1.48E-05		100	-1.29E-05	1.59E-05	
		previous year	37	0.0016	0.0012		44	0.0011	0.0014	
	August-October	**same year**	57	-0.0016	0.0010	.	89	0.0029	0.0012	*
		previous year	80	-0.0021	0.0010	*	39	-0.0012	0.0011	
interaction of warmth and rainfall (April-July, same year)			0	-	-		0	-	-	
interaction of warmth and rainfall squared (April-July, same year)			100	1.46E-07	4.51E-08	**	100	1.75E-07	4.93E-08	***

Summary of results for GLMs with ΔAIC < 4 (a set of 35 top models for *C. discolor* and 18 for *M. roeselii*). The importance of variables as predictors of colonisation rate is indicated by the proportion of top models in which they are included (% included), and by their coefficients and standard errors (weighted means across top models) and associated significance levels (sig: . = p<0.1, *=p<0.05, **=p<0.01, ***=p<0.001). Results are for the time period 1977 to 2012. Colonisations up to the 90th percentile of dispersal distances were considered ("maximum typical dispersal distance" of 23.5 km for *C. discolor* and 21.4 km for *M. roeselii*). Note that interacting terms have to be interpreted together (cf. Fig 4.4).

S 4.8 Table. Effects of weather on annual colonisation rates of *Conocephalus discolor* and *Metrioptera roeselii*, study period shortened to 1988-2012

			Conocephalus discolor				***Metrioptera roeselii***			
			% included	**weighted mean coefficient**	**weighted mean standard error**	**sig**	**% included**	**weighted mean coefficient**	**weighted mean standard error**	**sig**
(Intercept)			100	-6.7292	10.9054		100	-80.1283	20.0460	
year			42	0.0088	0.0105		100	0.0393	0.0102	***
warmth (GDD10)	**April-July**	**same year**	100	-0.0017	0.0026		100	-0.0009	0.0028	
		previous year	45	-0.0017	0.0015		23	0.0000	0.0017	
	August-October	**same year**	100	0.0053	0.0014	***	38	0.0017	0.0015	
		previous year	42	-0.0011	0.0013		69	0.0027	0.0014	.
rainfall (mm)	**April-July**	**same year**	100	-0.0149	0.0059	*	100	-0.0134	0.0061	*
		same year, squared	100	-2.23E-05	1.43E-05		100	-4.37E-06	1.51E-05	
		previous year	48	0.0019	0.0013		27	-0.0006	0.0013	
	August-October	**same year**	45	-0.0016	0.0010		35	0.0011	0.0012	
		previous year	94	-0.0023	0.0010	*	27	-0.0001	0.0011	
interaction of warmth and rainfall (April-July, same year)			0	-	-		0	-	-	
interaction of warmth and rainfall squared (April-July, same year)			100	1.42E-07	4.51E-08	**	92	9.27E-08	4.25E-08	*

Summary of results for GLMs with $\Delta\text{AIC} < 4$ (a set of 31 top models for *C. discolor* and 26 for *M. roeselii*). The importance of variables as predictors of colonisation rate is indicated by the proportion of top models in which they are included (% included), and by their coefficients and standard errors (weighted means across top models) and associated significance levels (sig: *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$). Results are for the time period 1988 to 2012; the start year was moved back from 1977 to 1988 in order to exclude all years with zero recorded hectad colonisations and cover only the years of continuous, positive range expansion. Colonisations up to the 95th percentile of dispersal distances were considered (“maximum typical dispersal distance” of 31.6 km for *C. discolor* and 29.9 km for *M. roeselii*). Note that interacting terms have to be interpreted together (cf. Fig 4.4).



S 4.1 Fig. Histogram of colonisation distances for *Conocephalus discolor* and *Metrioptera roeselii* between 1977 and 2012, including extinctions and re-colonisations.

Colonisation distance was defined as the distance between the centroid of a colonised or re-colonised hectad and the centroid of the nearest previously occupied hectad for the species. The focal species was assumed to have gone extinct in squares where it was not recorded in 4 years of visits, and any subsequent records were regarded as re-colonisations. The 95th percentile of colonisation distances (31.6km for *C. discolor* and 28.3km for *M. roeselii*) was defined as the "maximum typical dispersal distance" for subsequent calculations. Note log scale of y-axis.

S 4.9 Table. Effects of weather on annual colonisation rates of *Conocephalus discolor* and *Metrioptera roeselii*, including extinctions and re-colonisations

			Conocephalus discolor				***Metrioptera roeselii***			
			% included	**weighted mean coefficient**	**weighted mean standard error**	**sig**	**% included**	**weighted mean coefficient**	**weighted mean standard error**	**sig**
(Intercept)			100	-12.3220	13.9376		100	-93.5632	15.1727	
year			50	0.0105	0.0077		100	0.0468	0.0079	***
warmth (GDD10)	**April-July**	**same year**	100	-0.0016	0.0022		100	-0.0045	0.0028	
		previous year	38	-0.0007	0.0014		35	-0.0006	0.0015	
	August-October	**same year**	100	0.0055	0.0013	***	85	0.0032	0.0014	*
		previous year	38	0.0005	0.0012		73	0.0027	0.0013	*
rainfall (mm)	**April-July**	**same year**	100	-0.0128	0.0049	**	100	-0.0202	0.0061	***
		same year, squared	100	-2.17E-05	1.26E-05	.	100	-1.01E-05	1.44E-05	
		previous year	54	0.0020	0.0011	.	38	0.0014	0.0012	
	August-October	**same year**	54	-0.0014	0.0009		54	0.0016	0.0011	
		previous year	100	-0.0024	0.0009	**	42	-0.0003	0.0010	
interaction of warmth and rainfall (April-July, same year)			0	-	-		0	-	-	
interaction of warmth and rainfall squared (April-July, same year)			100	1.28E-07	3.73E-08	***	100	1.26E-07	4.58E-08	**

Summary of results for GLMs with ΔAIC < 4 (a set of 26 top models for both *C. discolor* and *M. roeselii*). The importance of variables as predictors of colonisation rate is indicated by the proportion of top models in which they are included (% included), and by their coefficients and standard errors (weighted means across top models) and associated significance levels (sig: . = p<0.1, *=p<0.05, **=p<0.01, ***=p<0.001). Results are for the time period 1977 to 2012. Colonisations up to the 95th percentile of dispersal distances were considered (“typical maximum dispersal distance” of 31.6 km for *C. discolor* and 28.3 km for *M. roeselii*). The focal species was assumed to have gone extinct in squares where it was not recorded in 4 years of visits, and any subsequent records were regarded as re-colonisations. Note that interacting terms have to be interpreted together (cf. Fig 4.4).

S 4.10 Table: Effects on population density of distance from range core and age of population

species	predictive variable	coefficient	SE	t	P	significance
Conocephalus discolor	distance from range core	5.66E-05	3.31E-04	0.171	0.865	n.s.
	age of population	2.32E-03	3.78E-03	0.613	0.543	n.s.
Metrioptera roeselii	distance from range core	-2.22E-03	1.80E-03	-1.238	0.229	n.s.
	age of population	1.67E-02	6.51E-03	2.567	0.018	*

Results of linear models of distance from range core (km) and age of population (years) against population density (individuals found per minute) for *Conocephalus discolor* and *Metrioptera roeselii* during field surveys during 2008-12 (see S 4.2 and S 4.3 Tables for data).

References

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control **19**:716-723.

Altermatt, F. 2010. Climatic warming increases voltinism in European butterflies and moths. Proceedings of the Royal Society B: Biological Sciences **277**:1281-1287.

Ando, Y. and J. C. Hartley. 1982. Occurrence and biology of a long-winged form of *Conocephalus discolor*. Entomologia experimentalis et applicata **32**:238-241.

Angert, A. L., L. G. Crozier, L. J. Rissler, S. E. Gilman, J. J. Tewksbury, and A. J. Chunco. 2011. Do species' traits predict recent shifts at expanding range edges? Ecology Letters **14**:677–689.

August, T. 2015. sparta - Species Presence/Absence R Trends Analyses, vignette. https://github.com/BiologicalRecordsCentre/sparta/raw/master/vignettes/sparta_vignette.pdf.

August, T., M. Harvey, P. Lightfoot, D. Kilbey, T. Papadopoulos, and P. Jepson. 2015a. Emerging technologies for biological recording. Biological Journal of the Linnean Society **115**:731-749.

August, T., G. Powney, C. Harrower, M. Hill, and N. Isaac. 2015b. sparta: Trend Analysis for Unstructured Data. R package version 0.1.30. https://github.com/biologicalrecordscentre/sparta.

Ausden, M. 1996. Invertebrates. *in* W. J. Sutherland, editor. Ecological Census Techniques: A Handbook. Cambridge University Press, Cambridge.

Baker, E., B. W. Price, S. D. Rycroft, J. Hill, and V. S. Smith. 2015. BioAcoustica: a free and open repository and analysis platform for bioacoustics. Database **2015**:bav054.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology **8**:1-16.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software **67**:1-48.

Beckmann, B. C. 2013. Identification guides to grasshoppers, bush-crickets, earwigs, cockroaches and stick-insects. http://www.orthoptera.org.uk/node/1035

Beckmann, B. C. 2017. Orthoptera county atlases. Forum post on Orthoptera Recording Scheme website. Retrieved 2/1/2017 from www.orthoptera.org.uk/node/364

Beckmann, B. C., B. V. Purse, D. B. Roy, H. E. Roy, P. G. Sutton, and C. D. Thomas. 2015. Two Species with an Unusual Combination of Traits Dominate Responses of British Grasshoppers and Crickets to Environmental Change. PLoS One **10**:e0130488.

Beckmann, B. C. and P. Sutton. 2013. Orthoptera Recording Scheme Newsletter No. 29. www.orthoptera.org.uk/Recording/index.php?q=newsletters

Behrens, M. and T. Fartmann. 2004. Sind hohe Populationsdichten die Ursache der Makropterie beim Gemeinen Grashüpfer (Chorthippus parallelus; Caelifera: Acrididae). Articulata **19**:91-102.

Bennie, J., J. A. Hodgson, C. R. Lawson, C. T. R. Holloway, D. B. Roy, T. Brereton, C. D. Thomas, and R. J. Wilson. 2013. Range expansion through fragmented landscapes under a variable climate. Ecology Letters **16**:921-929.

Benton, T. 2012. New Naturalist Library (120) - Grasshoppers and Crickets. Collins, London.

Bishop, T. R., M. S. Botham, R. Fox, S. R. Leather, D. S. Chapman, and T. H. Oliver. 2013. The utility of distribution data in predicting phenology. Methods in Ecology and Evolution **4**:1024-1032.

Blockeel, T. L., S. D. S. Bosanquet, M. O. Hill, and C. D. Preston. 2014. Atlas of British & Irish Bryophytes. NatureBureau, Newbury.

Bogaart, P., M. van der Loo, and J. Pannekoek. 2016. rtrim: Trends and Indices for Monitoring Data. R package version 1.0.1. https://CRAN.R-project.org/package=rtrim

Bonney, R., C. B. Cooper, J. Dickinson, S. Kelling, T. Phillips, K. V. Rosenberg, and J. Shirk. 2009. Citizen science: a developing tool for expanding science knowledge and scientific literacy. BioScience **59**:977-984.

Brereton, T., K. Cruickshanks, K. Risely, D. Noble, and D. Roy. 2011. Developing and launching a wider countryside butterfly survey across the United Kingdom. Journal of Insect Conservation **15**:279-290.

Brereton, T. M., M. S. Botham, I. Middlebrook, Z. Randle, N. D., and D. B. Roy. 2016. United Kingdom Butterfly Monitoring Scheme report for 2015. Centre for Ecology & Hydrology & Butterfly Conservation.

Brickle, N. W., D. G. Harper, N. J. Aebischer, and S. H. Cockayne. 2000. Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. Journal of Applied Ecology **37**:742-755.

Bried, J. T. and J. Pellet. 2012. Optimal design of butterfly occupancy surveys and testing if occupancy converts to abundance for sparse populations. Journal of Insect Conservation **16**:489-499.

Brown, J. and M. Lomolino. 1998. Biogeography, 2nd ed. Sinauer Associates, Sunderland, Massachusetts.

BTO. 2011. The Breeding Bird Survey: Methodology and survey design: Analytical methods. https://www.bto.org/volunteer-surveys/bbs/research-conservation/methodology

Buckley, L. B. and J. G. Kingsolver. 2012. Functional and phylogenetic approaches to forecasting species' responses to climate change. Annual Review of Ecology, Evolution and Systematics **43**:205-226.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Burns, F., M. A. Eaton, K. E. Barlow, B. C. Beckmann, T. Brereton, D. R. Brooks, P. M. Brown, N. Al Fulaij, T. Gent, and I. Henderson. 2016. Agricultural management and climatic change are the major drivers of biodiversity change in the UK. PLoS One **11**:e0151595.

Burton, J. F. 2003. The apparent influence of climatic change on recent changes of range by European insects (Lepidoptera, Orthoptera). Proceedings of the 13th International Colloquium of the European Invertebrate Survey (EIS):13-21.

Burton, O. J., B. L. Phillips, and J. M. Travis. 2010. Trade-offs and the evolution of life-histories during range expansion. Ecology Letters **13**:1210-1220.

Carey, P. D., S. Wallis, P. M. Chamberlain, A. Cooper, B. A. Emmett, L. C. Maskell, T. McCann, J. Murphy, L. R. Norton, B. Reynolds, W. A. Scott, I. C. Simpson, S. M. Smart, and J. M. Ullyett. 2008. Countryside Survey: UK Results from 2007. NERC/Centre for Ecology & Hydrology.

Carson, R. 1962. Silent Spring. Houghton Mifflin, Boston, MA.

Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. Biological Conservation **103**:33-49.

Carvell, C., N. J. B. Isaac, M. Jitlal, J. Peyton, G. D. Powney, D. B. Roy, A. J. Vanbergen, R. S. O'Connor, C. M. Jones, W. E. Kunin, T. D. Breeze, M. P. D. Garratt, S. G. Potts, M. Harvey, J. Ansine, R. F. Comont, P. Lee, M. Edwards, S. P. M. Roberts, R. K. A. Morris, A. J. Musgrove, T. Brereton, C. Hawes, and H. E. Roy. 2016. Design and Testing of a National Pollinator and Pollination Monitoring Framework. Final summary report to the Department for Environment, Food and Rural Affairs (Defra), Scottish Government and Welsh Government: Project WC1101.

Chapman, A. D. 2009. Numbers of living species in Australia and the world: A report for the Australian Biological Resources Study. Australian Biodiversity Information Services, Toowoomba, Australia.

Chapman, J. W., D. R. Reynolds, A. D. Smith, J. R. Riley, D. E. Pedgley, and I. P. Woiwod. 2002. High-altitude migration of the diamondback moth Plutella xylostella to the U.K.: a study using radar, aerial netting, and ground trapping. Ecological Entomology **27**:641-650.

Chatfield, C. 2003. The analysis of time series : an introduction. Chapman & Hall/CRC, Boca Raton, FL.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science **333**:1024-1026.

Chen, I.-C., H.-J. Shiu, S. Benedick, J. D. Holloway, V. K. Chey, H. S. Barlow, J. K. Hill, and C. D. Thomas. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. Proceedings of the National Academy of Sciences **106**:1479-1483.

Cherrill, A. 2010. Species richness of Orthoptera along gradients of agricultural intensification and urbanisation. Journal of Orthoptera Research **19**:293-301.

Cherrill, A. J. 1993. The conservation of Britain's wart-biter bush-crickets. British Wildlife **5**:26-32.

Chesmore, E. and E. Ohya. 2004. Automated identification of field-recorded songs of four British grasshoppers using bioacoustic signal recognition. Bulletin of Entomological Research **94**:319-330.

Cigliano, M. M., H. Braun, D. C. Eades, and D. Otte. 2017. Orthoptera Species File. Version 5.0/5.0. Retrieved 25/01/2017 from http://Orthoptera.SpeciesFile.org

Cleveland, W. S. 1981. LOWESS: A program for smoothing scatterplots by robust locally weighted regression. The American Statistician **35**:54.

Clobert, J., M. Baguette, T. G. Benton, J. M. Bullock, and S. Ducatez. 2012. Dispersal ecology and evolution. Oxford University Press, Oxford.

Comont, R. F., H. E. Roy, O. T. Lewis, R. Harrington, C. R. Shortall, and B. V. Purse. 2012. Using biological traits to explain ladybird distribution patterns. Journal of Biogeography **39**:1772-1781.

Conrad, K. F., I. P. Woiwod, M. Parsons, R. Fox, and M. S. Warren. 2004. Long-term population trends in widespread British moths. Journal of Insect Conservation **8**:119-136.

Cowley, M., C. Thomas, D. Roy, R. Wilson, J. León-Cortés, D. Gutiérrez, C. Bulman, R. Quinn, D. Moss, and K. Gaston. 2001a. Density–distribution relationships in British butterflies. I. The effect of mobility and spatial scale. Journal of animal ecology **70**:410-425.

Cowley, M., C. Thomas, J. Thomas, and M. Warren. 1999. Flight areas of British butterflies: assessing species status and decline. Proceedings of the Royal Society of London B: Biological Sciences **266**:1587-1592.

Cowley, M., C. Thomas, R. Wilson, J. León-Cortés, D. Gutiérrez, and C. Bulman. 2001b. Density–distribution relationships in British butterflies. II. An assessment of mechanisms. Journal of animal ecology **70**:426-441.

Crawley, M. J. 2007. The R book. John Wiley & Sons Ltd, Chichester.

Crozier, R. H., L. J. Dunnett, and P.-M. Agapow. 2005. Phylogenetic biodiversity assessment based on systematic nomenclature. Evolutionary Bioinformatics Online **1**:11-36.

Crutzen, P. J. 2002. Geology of mankind. Nature **415**:23-23.

Curry, J. P. 1994. Grassland Invertebrates: ecology, influence on soil fertility and effects on plant growth. Chapman & Hall, London.

Dapporto, L. and R. L. H. Dennis. 2013. The generalist–specialist continuum: Testing predictions for distribution and trends in British butterflies. Biological Conservation **157**:229-236.

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

Davies, Z. G., R. J. Wilson, S. Coles, and C. D. Thomas. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. Journal of animal ecology **75**:247-256.

Defra. 2010. Department for Environment Food and Rural Affairs: June Survey of Agriculture and Horticulture: England timeseries 1983-2010. Retrieved 20/02/2014 from http://archive.defra.gov.uk/evidence/statistics/foodfarm/landuselivestock/junesurvey/documents/England-timeseries.xls

Defra. 2015. Department for Environment Food and Rural Affairs: Organic farming statistics 2014. Retrieved 28/02/2017 from www.gov.uk/government/uploads/system/uploads/attachment_data/file/444287/organics-statsnotice-23jun15b.pdf

Defra. 2016. Department for Environment Food and Rural Affairs: Observatory monitoring framework: Indicator C2: Agricultural land use. Retrieved 28/02/2017 from www.gov.uk/government/uploads/system/uploads/attachment_data/file/541591/agindicator-c2-29jul16.pdf

Delf, J. 2013. Diapause and polymorphism in the Long-winged Conehead *Conocephalus discolor.* Talk given at the Royal Entomological Society Special Interest Group on Orthoptera meeting in the Natural History Museum London.

Dennis, E. B., B. J. Morgan, S. N. Freeman, T. M. Brereton, and D. B. Roy. 2016. A generalized abundance index for seasonal invertebrates. Biometrics **72**:1305-1314.

Detzel, P. 1998. Die Heuschrecken Baden-Württembergs. Verlag Eugen Ulmer, Stuttgart.

Deura, K. and J. C. Hartley. 1982. Initial diapause and embryonic development in the speckled bush-cricket, *Leptophyes punctatissima*. Physiological Entomology **7**:253-262.

Dickinson, J. L. and R. Bonney, editors. 2012. Citizen science: Public participation in environmental research. Cornell University Press, Ithaca.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, and P. J. Leitão. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography **36**:27-46.

Dudley, R. 2002. The biomechanics of insect flight: form, function, evolution. Princeton University Press, Princeton, New Jersey.

Dziock, F., M. Gerisch, M. Siegert, I. Hering, M. Scholz, and R. Ernst. 2011. Reproducing or dispersing? Using trait based habitat templet models to analyse Orthoptera response to flooding and land use. Agriculture, Ecosystems & Environment **145**:85-94.

Eades, D. C., D. Otte, M. M. Cigliano, and H. Braun. 2013. Orthoptera Species File. Retrieved 03/10/2013 from http://orthoptera.speciesfile.org/HomePage.aspx

Eaton, M. A., F. Burns, N. J. Isaac, R. D. Gregory, T. A. August, K. E. Barlow, T. Brereton, D. R. Brooks, N. Al Fulaij, and K. A. Haysom. 2015. The priority species indicator: measuring the trends in threatened species in the UK. Biodiversity **16**:108-119.

Edwards, M. 2008. English Nature Species Recovery Programme, Field Cricket, *Gryllus campestris*, Project Report for 2008. Natural England, Peterborough.

Edwards, M., J. M. Patmore, and D. Sheppard. 1996. The field cricket - preventing extinction. British Wildlife **8**:87-91.

Emlen, D. J. 2001. Costs and the diversification of exaggerated animal structures. Science **291**:1534-1536.

Enfjäll, K. and O. Leimar. 2005. Density-dependent dispersal in the Glanville fritillary, *Melitaea cinxia*. Oikos **108**:465-472.

Evans, A., K. Smith, D. Buckingham, and J. Evans. 1997. Seasonal variation in breeding performance and nestling diet of cirl buntings *Emberiza cirlus* in England. Bird Study **44**:66-79.

Evans, M. and R. Edmondson. 2007. A Photographic Guide to the Grasshoppers & Crickets of Great Britain & Ireland. Wild Guide UK (WGUK), Bristol.

FAO. 2016. Global Forest Resources Assessment 2015: How are the world's forests changing? Second edition., Food and Agriculture Organisation of the United Nations, Rome.

Fischer, F. P., U. Schulz, H. Schubert, P. Knapp, and M. Schmöger. 1997. Quantitative assessment of grassland quality: acoustic determination of population sizes of Orthopteran indicator species. Ecological Applications **7**:909-920.

Fischer, J., D. Steinlechner, A. Zehm, D. Poniatowski, T. Fartmann, A. Beckmann, and C. Stettmer. 2016. Die Heuschrecken Deutschlands und Nordtirols. Quelle & Meyer, Wiebelsheim.

Fox, R., T. Brereton, J. Asher, T. August, M. Botham, N. Bourn, K. Cruickshanks, C. Bulman, S. Ellis, C. Harrower, I. Middlebrook, D. G. Noble, G. D. Powney, Z. Randle, M. S. Warren, and D. B. Roy. 2015. The State of the UK's Butterflies 2015. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, Dorset.

Fox, R., T. H. Oliver, C. Harrower, M. S. Parsons, C. D. Thomas, and D. B. Roy. 2014. Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. Journal of Applied Ecology **51**:949–957.

Franco, A., J. K. Hill, C. Kitschke, Y. C. Collingham, D. B. Roy, R. Fox, B. Huntley, and C. D. Thomas. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. Global Change Biology **12**:1545-1553.

Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. The American Naturalist **160**:712-726.

Fuller, R. J., L. R. Norton, R. E. Feber, P. J. Johnson, D. E. Chamberlain, A. C. Joys, F. Mathews, R. C. Stuart, M. C. Townsend, W. J. Manley, M. S. Wolfe, D. W. Macdonald, and L. G. Firbank. 2005. Benefits of organic farming to biodiversity vary among taxa. Biology Letters **1**:431.

Gallagher, A. J., N. Hammerschlag, S. J. Cooke, D. P. Costa, and D. J. Irschick. 2015. Evolutionary theory as a tool for predicting extinction risk. Trends in Ecology & Evolution **30**:61-65.

Gardiner, T. 2009. Macropterism of Roesel's Bushcricket *Metrioptera roeselii* in Relation to Climate Change and Landscape Structure in Eastern England. Journal of Orthoptera Research **18**:95-102.

Gardiner, T. and J. Hill. 2004. Feeding preferences of *Chorthippus parallelus* (Orthoptera: Acrididae). Journal of Orthoptera Research **13**:197-203.

Gardiner, T. and J. Hill. 2006. A comparison of three sampling techniques used to estimate the population density and assemblage diversity of Orthoptera. Journal of Orthoptera Research **15**:45-51.

Gardiner, T., J. Hill, and D. Chesmore. 2005. Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems. Journal of Insect Conservation **9**:151-173.

Gardiner, T., M. Pye, R. Field, and J. Hill. 2002. The influence of sward height and vegetation composition in determining the habitat preferences of three Chorthippus species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. Journal of Orthoptera Research **11**:207-213.

Gaston, K. J. 2003. The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford.

Gibbs, J. P., S. Droege, and P. Eagle. 1998. Monitoring Populations of Plants and Animals. BioScience **48**:935-940.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. Trends in Ecology & Evolution **25**:325-331.

Glutz von Blotzheim, U. N., K. Bauer, and E. Bezzel, editors. 1973-1993. Handbuch der Vögel Mitteleuropas. Akademische Verlagsgesellschaft, Wiesbaden.

Gorochov, A. V. and J. A. Marshall. 2001. New data on *Pseudomogoplistes* from Atlantic islands (Orthoptera: Mogoplistidae). Zoosystematica Rossica **9**:76.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences **326**:119-157.

Guisan, A. and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135**:147-186.

Gullan, P. J. and P. S. Cranston. 1994. The insects: an outline of entomology. Chapman & Hall, London.

Haddad, N. M. and J. G. Kingsolver. 1999. Corridor use predicted from behaviors at habitat boundaries. The American Naturalist **153**:215-227.

Haes, E. C. M., editor. 1979. Provisional atlas of the insects of the British Isles. Part 6 Orthoptera: Grasshoppers and Crickets. 2nd edition. Biological Records Centre, Institute of Terrestrial Ecology, Abbots Ripton, Huntingdon.

Haes, E. C. M. and P. T. Harding. 1997. Atlas of Grasshoppers, Crickets and Allied Insects in Britain and Ireland. Stationery Office, London.

Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C. O. Justice, and J. R. G. Townshend. 2013. High-resolution global maps of 21st-century forest cover change. Science **342**:850-853.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford.

Hanski, I. 2015. Habitat fragmentation and species richness. Journal of Biogeography **42**:989-993.

Hanski, I., C. J. Breuker, K. Schöps, R. Setchfield, and M. Nieminen. 2002. Population history and life history influence the migration rate of female Glanville fritillary butterflies. Oikos **98**:87-97.

Harris, S. and D. W. Yalden. 2008. Mammals of the British Isles Handbook - 4th ed. The Mammal Society, Southampton.

Harris, S. J., D. Massimino, S. E. Newson, M. A. Eaton, J. H. Marchant, D. E. Balmer, D. G. Noble, S. Gillings, D. Procter, and J. W. Pearce-Higgins. 2016. The Breeding Bird Survey 2015. BTO Research Report 687. British Trust for Ornithology, Thetford.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society **42**:73-88.

Hassall, C., D. J. Thompson, and I. F. Harvey. 2009. Variation in morphology between core and marginal populations of three British damselflies. Aquatic Insects **31**:187-197.

Hayhow, D., F. Burns, M. Eaton, N. Al Fulaij, T. August, L. Babey, L. Bacon, C. Bingham, J. Boswell, K. Boughey, T. Brereton, E. Brookman, D. Brooks, D. Bullock, O. Burke, M. Collis, L. Corbet, N. Cornish, S. De Massimi, J. Densham, E. Dunn, S. Elliott, T. Gent, J. Godber, S. Hamilton, S. Havery, S. Hawkins, J. Henney, K. Holmes, N. Hutchinson, N. Isaac, D. Johns, C. Macadam, F. Mathews, P. Nicolet, D. Noble, C. Outhwaite, G. Powney, P. Richardson, D. Roy, D. Sims, S. Smart, K. Stevenson, R. Stroud, K. Walker, J. Webb, T. Webb, R. Wynde, and R. Gregory. 2016. State of Nature 2016., The State of Nature partnership.

Hendriks, R. J. J., L. G. Carvalheiro, R. M. J. C. Kleukers, and J. C. Biesmeijer. 2013. Temporal-spatial dynamics in Orthoptera in relation to nutrient availability and plant species richness. PLoS One **8**:e71736.

Henry, R. C., G. Bocedi, C. Dytham, and J. M. Travis. 2014. Inter-annual variability influences the eco-evolutionary dynamics of range-shifting. PeerJ **1**:e228.

Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology **12**:450-455.

Hill, J. K., Y. C. Collingham, C. D. Thomas, D. S. Blakeley, R. Fox, D. Moss, and B. Huntley. 2001. Impacts of landscape structure on butterfly range expansion. Ecology Letters **4**:313-321.

Hill, J. K., H. M. Griffiths, and C. D. Thomas. 2011. Climate change and evolutionary adaptations at species' range margins. Annual Review of Entomology **56**:143-159.

Hill, J. K., C. D. Thomas, and D. S. Blakeley. 1999. Evolution of flight morphology in a butterfly that has recently expanded its geographic range. Oecologia **121**:165-170.

Hochachka, W. M., D. Fink, R. A. Hutchinson, D. Sheldon, W.-K. Wong, and S. Kelling. 2012. Data-intensive science applied to broad-scale citizen science. Trends in Ecology & Evolution **27**:130-137.

Hochkirch, A. and M. Damerau. 2009. Rapid range expansion of a wing-dimorphic bush-cricket after the 2003 climatic anomaly. Biological Journal of the Linnean Society **97**:118-127.

Hochkirch, A., A. Nieto, M. García Criado, M. Cálix, Y. Braud, F. M. Buzzetti, D. Chobanov, B. Odé, J. J. Presa Asensio, L. Willemse, and T. Zuna-Kratky. 2016. European Red List of Grasshoppers, Crickets and Bush-crickets. Publications Office of the European Union, Luxembourg.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics **6**:65-70.

Ingrisch, S. 1984. The influence of environmental factors on dormancy and duration of egg development in *Metrioptera roeseli* (Orthoptera: Tettigoniidae). Oecologia **61**:254-258.

Ingrisch, S. and G. Köhler. 1998. Die Heuschrecken Mitteleuropas. Westarp Wissenschaften, Magdeburg.

IPCC. 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Isaac, N. J. and M. J. Pocock. 2015. Bias and information in biological records. Biological Journal of the Linnean Society **115**:522-531.

Isaac, N. J. B., A. J. van Strien, T. A. August, M. P. Zeeuw, and D. B. Roy. 2014. Statistics for citizen science: extracting signals of change from noisy ecological data. Methods in Ecology and Evolution **5**:1052-1060.

IUCN. 2012. IUCN Red List Categories and Criteria. Version 3.1., IUCN Species Survival Commission, Gland, Switzerland.

Jeliazkov, A., Y. Bas, C. Kerbiriou, J.-F. Julien, C. Penone, and I. Le Viol. 2016. Large-scale semi-automated acoustic monitoring allows to detect temporal decline of bush-crickets. Global Ecology and Conservation **6**:208-218.

Jones, H. B., K. S. Lim, J. R. Bell, J. K. Hill, and J. W. Chapman. 2016. Quantifying interspecific variation in dispersal ability of noctuid moths using an advanced tethered flight technique. Ecology and Evolution **6**:181-190.

Kallioniemi, E., A. Zannese, J. E. Tinker, and A. Franco. 2014. Inter-and intra-specific differences in butterfly behaviour at boundaries. Insect Conservation and Diversity **7**:232-240.

Kaňuch, P., Å. Berggren, and A. Cassel-Lundhagen. 2014. Genetic diversity of a successful colonizer: isolated populations of Metrioptera roeselii regain variation at an unusually rapid rate. Ecology and Evolution **4**:1117-1126.

Kaňuch, P., Å. Berggren, and A. Cassel-Lundhagen. 2013. Colonization history of Metrioptera roeselii in northern Europe indicates human-mediated dispersal. Journal of Biogeography **40**:977-987.

Kéry, M. and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, MA.

Kindvall, O., K. Vessby, Å. Berggren, and G. Hartman. 1998. Individual mobility prevents an Allee effect in sparse populations of the bush cricket *Metrioptera roeseli*: an experimental study. Oikos:449-457.

Kleukers, R. M. J. C., K. Decleer, E. C. M. Haes, P. Kolshorn, and B. Thomas. 1996. The recent expansion of *Conocephalus discolor* (Thunberg) (Orthoptera: Tettigoniidae) in western Europe. Entomologist's Gazette **47**:37-50.

Krall, S., R. Peveling, and D. Ba Diallo. 1998. New Strategies in Locust Control. Birkhäuser Verlag, Basel.

Kuussaari, M., M. Nieminen, and I. Hanski. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. Journal of animal ecology **65**:791-801.

Le Galliard, J., M. Massot, and J. Clobert. 2012. Dispersal and range dynamics in changing climates: a review. *in* J. Clobert, M. Baguette, T. G. Benton, and D. Bullock, editors. Dispersal Ecology and Evolution. Oxford University Press, Oxford.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America **15**:237-240.

Levins, R. 1970. Extinction. *in* M. Gerstenhaber, editor. Lectures on Mathematics in the Life Sciences, Vol 2: Some Mathematical Questions in Biology. American Mathematical Society, Providence, Rhode Island.

Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2013. Invasion Ecology. John Wiley & Sons, Chichester, UK.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

Mace, G. M., N. J. Collar, K. J. Gaston, C. Hilton-Taylor, H. R. Akçakaya, N. Leader-Williams, E. J. Milner-Gulland, and S. N. Stuart. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. Conservation Biology **22**:1424-1442.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology **84**:2200-2207.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**:2248-2255.

Mair, L., J. K. Hill, R. Fox, M. Botham, T. Brereton, and C. D. Thomas. 2014. Abundance changes and habitat availability drive species' responses to climate change. Nature Climate Change **4**:127-131.

Mair, L., C. D. Thomas, B. J. Anderson, R. Fox, M. Botham, and J. K. Hill. 2012. Temporal variation in responses of species to four decades of climate warming. Global Change Biology **18**:2439-2447.

Mair, L., C. D. Thomas, A. Franco, and J. K. Hill. 2015. Quantifying the activity levels and behavioural responses of butterfly species to habitat boundaries. Ecological Entomology **40**:823-828.

Marini, L., R. Bommarco, P. Fontana, and A. Battisti. 2010. Disentangling effects of habitat diversity and area on orthopteran species with contrasting mobility. Biological Conservation **143**:2164-2171.

Marshall, J. A. and E. C. M. Haes. 1988. Grasshoppers and Allied Insects of Great Britain and Ireland. Harley Books, Colchester.

Marshall, J. A. and D. Ovenden. 1999. Guide to British grasshoppers and allied insects. AIDGAP foldout chart., Field Studies Council, Preston Montford.

Mason, S. C., G. Palmer, R. Fox, S. Gillings, J. K. Hill, C. D. Thomas, and T. H. Oliver. 2015. Geographical range margins of many taxonomic groups continue to shift polewards. Biological Journal of the Linnean Society **115**:586-597.

Maxmen, A. 2013. Crop pests: Under attack. Nature **501**:S15-S17.

McCarty, J. P. 2001. Ecological consequences of recent climate change. Conservation Biology **15**:320-331.

McMaster, G. S. and W. Wilhelm. 1997. Growing degree-days: one equation, two interpretations. Agricultural and Forest Meteorology **87**:291-300.

Mearns, R. and M. Marquiss. 2016. Short-winged Cone-heads *Conocephalus dorsalis* in Scotland. *in* B. C. Beckmann and P. Sutton, editors. Grasshoppers and related species Recording Scheme of Britain and Ireland Newsletter 33, Autumn 2016.

Meineke, T. 1994. Ausbreitungsversuche und initiale Populationsstadien von *Chorthippus parallelus* (Zetterstedt) im Hochharz. Articulata **9**:33-42.

Merrill, R. M., D. Gutiérrez, O. T. Lewis, J. Gutiérrez, S. B. Díez, and R. J. Wilson. 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. Journal of animal ecology **77**:145-155.

Millennium Ecosystem Assessment. 2005a. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

Millennium Ecosystem Assessment. 2005b. Policy Responses: Chapter 9 - Nutrient Management. World Resources Institute, Washington, DC.

Miller-Rushing, A., R. Primack, and R. Bonney. 2012. The history of public participation in ecological research. Frontiers in Ecology and the Environment **10**:285-290.

Miner, B. G., S. E. Sultan, S. G. Morgan, D. K. Padilla, and R. A. Relyea. 2005. Ecological consequences of phenotypic plasticity. Trends in Ecology & Evolution **20**:685-692.

Moran, P. A. P. 1950. Notes on continuous stochastic phenomena. Biometrika **37**:17-23.

Morecroft, M. D. and L. Speakman. 2015. Biodiversity Climate Change Impacts Summary Report., Living With Environmental Change (LWEC) partnership, Peterborough.

Murphy, J. M., D. M. H. Sexton, G. J. Jenkins, P. M. Boorman, B. B. B. Booth, C. C. Brown, R. T. Clark, M. Collins, G. R. Harris, E. J. Kendon, R. A. Betts, S. J. Brown, T. P. Howard, K. A. Humphrey, M. P. McCarthy, R. E. McDonald, A. Stephens, C. Wallace, R. Warren, R. Wilby, and R. A. Wood. 2009. UK Climate Projections Science Report: Climate change projections. Met Office Hadley Centre, Exeter.

NASA. 2017. NASA, NOAA Data Show 2016 Warmest Year on Record Globally. Retrieved 27/02/2017 from www.nasa.gov/press-release/nasa-noaa-data-show-2016-warmest-year-on-record-globally

Nathan, R., E. Klein, J. J. Robledo-Arnuncio, and E. Revilla. 2012. Dispersal kernels: review. *in* J. Clobert, M. Baguette, T. G. Benton, and J. M. Bullock, editors. Dispersal Ecology and Evolution. Oxford University Press, Oxford.

National Biodiversity Network. 2017. NBN Atlas. Retrieved 07/04/2017 from https://nbnatlas.org

Newson, S. E., Y. Bas, A. Murray, and S. Gillings. 2017. Potential for coupling the monitoring of bush-crickets with established large-scale acoustic monitoring of bats. Methods in Ecology and Evolution: article not yet assigned to an issue.

Nielsen, E. T. and H. Dreisig. 1970. The behavior of stridulation in Orthoptera Ensifera. Behaviour **37**:205-251.

O'Neill, K. M., D. P. Larson, and W. P. Kemp. 2002. Sweep sampling technique affects estimates of the relative abundance and community composition of grasshoppers (Orthoptera: Acrididae). Journal of Agricultural and Urban Entomology **19**:125-131.

Oaks, J. L., M. Gilbert, M. Z. Virani, R. T. Watson, C. U. Meteyer, B. A. Rideout, H. Shivaprasad, S. Ahmed, M. J. I. Chaudhry, and M. Arshad. 2004. Diclofenac residues as the cause of vulture population decline in Pakistan. Nature **427**:630-633.

Öckinger, E., O. Schweiger, T. O. Crist, D. M. Debinski, J. Krauss, M. Kuussaari, J. D. Petersen, J. Poyry, J. Settele, K. S. Summerville, and R. Bommarco. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters **13**:969-979.

Ofcom. 2016. Statistics and facts on the communications industry taken from Ofcom research publications. Retrieved 15/10/2016 from https://www.ofcom.org.uk/about-ofcom/latest/media/facts

Oliver, T., J. K. Hill, C. D. Thomas, T. Brereton, and D. B. Roy. 2009. Changes in habitat specificity of species at their climatic range boundaries. Ecology Letters **12**:1091-1102.

Oliver, T. H., N. J. Isaac, T. A. August, B. A. Woodcock, D. B. Roy, and J. M. Bullock. 2015a. Declining resilience of ecosystem functions under biodiversity loss. Nature Communications **6**:10122.

Oliver, T. H., H. H. Marshall, M. D. Morecroft, T. Brereton, C. Prudhomme, and C. Huntingford. 2015b. Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. Nature Climate Change **5**:941-945.

Oliver, T. H., C. D. Thomas, J. K. Hill, T. Brereton, and D. B. Roy. 2012. Habitat associations of thermophilous butterflies are reduced despite climatic warming. Global Change Biology **18**:2720-2729.

Orme, D., R. Freckleton, G. Thomas, T. Petzoldt, S. Fritz, N. Isaac, and W. Pearse. 2013. caper - Comparative Analyses of Phylogenetics and Evolution in R. http://cran.r-project.org/web/packages/caper/index.html

Orthoptera and Allied Insects Recording Scheme of Britain and Ireland. 2014. www.orthoptera.org.uk

Orthoptera Recording Scheme. 2013a. Grasshopper and Cricket (Orthoptera) and related species records from Britain and Ireland to 2007. Retrieved 08/05/2015 from https://data.nbn.org.uk/Datasets/GA000157

Orthoptera Recording Scheme. 2013b. Orthoptera and Allied Insects of the British Isles data from iRecord. Retrieved 08/05/2015 from https://data.nbn.org.uk/Datasets/GA001180

Orthoptera Recording Scheme. 2015a. Grasshopper and Cricket (Orthoptera) and related species records from Britain and Ireland. Retrieved 12/08/2016 from https://data.nbn.org.uk/Datasets/GA000157

Orthoptera Recording Scheme. 2015b. Orthoptera and Allied Insects of the British Isles data from iRecord. Retrieved 08/05/2015 from https://data.nbn.org.uk/Datasets/GA001180

Oschmann, M. 1991. Zur Klassifizierung der ökologischen Ansprüche von Schaben (Blattodea) und Heuschrecken (Orthoptera). Faunistische Abhandlungen des Staatlichen Museums für Tierkunde Dresden **18**:51-57.

Oswald, P. and C. D. Preston. 2011. John Ray's Cambridge Catalogue (1660). Ray Society.

Pagel, J., B. J. Anderson, R. B. O'Hara, W. Cramer, R. Fox, F. Jeltsch, D. B. Roy, C. D. Thomas, and F. M. Schurr. 2014. Quantifying range-wide variation in population trends from local abundance surveys and widespread opportunistic occurrence records. Methods in Ecology and Evolution **5**:751-760.

Paradis, E. 2011. Analysis of Phylogenetics and Evolution with R. Springer, New York.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics **20**:289-290.

Parker, D. and B. Horton. 2005. Uncertainties in central England temperature 1878–2003 and some improvements to the maximum and minimum series. International Journal of Climatology **25**:1173-1188.

Parker, D. E., T. P. Legg, and C. K. Folland. 1992. A new daily Central England Temperature Series, 1772-1991. International Journal of Climatology **12**:317-342.

Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, and T. Tammaru. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature **399**:579-583.

Parton, W., J. Morgan, D. Smith, S. Del Grosso, L. Prihodko, D. LeCain, R. Kelly, and S. Lutz. 2012. Impact of precipitation dynamics on net ecosystem productivity. Global Change Biology **18**:915-927.

Pateman, R. M., J. K. Hill, D. B. Roy, R. Fox, and C. D. Thomas. 2012. Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. Science **336**:1028-1030.

Pateman, R. M., C. D. Thomas, S. A. Hayward, and J. K. Hill. 2016. Macro-and microclimatic interactions can drive variation in species' habitat associations. Global Change Biology **22**:556-566.

Pearce-Kelly, P., R. Jones, D. Clarke, C. Walker, P. Atkin, and A. Cunningham. 1998. The captive rearing of threatened Orthoptera: a comparison of the conservation potential and practical considerations of two species' breeding programmes at the Zoological Society of London. Journal of Insect Conservation **2**:201-210.

Pellet, J., J. T. Bried, D. Parietti, A. Gander, P. O. Heer, D. Cherix, and R. Arlettaz. 2012. Monitoring butterfly abundance: beyond Pollard walks. PLoS One **7**:e41396.

Penone, C., I. Le Viol, V. Pellissier, J. F. Julien, Y. Bas, and C. Kerbiriou. 2013. Use of Large-Scale Acoustic Monitoring to Assess Anthropogenic Pressures on Orthoptera Communities. Conservation Biology **27**:979-987.

Perring, F. H. and S. M. Walters, editors. 1962. Atlas of the British flora. Thomas Nelson & Sons, London.

Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate Change and Distribution Shifts in Marine Fishes. Science **308**:1912-1915.

Pescott, O., M. Jitlal, S. Smart, K. Walker, D. Roy, and S. Freeman. 2016. A comparison of models for interval-censored plant cover data, with applications to monitoring schemes. PeerJ Preprints **4**:e2532v2531.

Pescott, O. L., K. J. Walker, M. J. O. Pocock, M. Jitlal, C. L. Outhwaite, C. M. Cheffings, F. Harris, and D. B. Roy. 2015. Ecological monitoring with citizen science: the design and implementation of schemes for recording plants in Britain and Ireland. Biological Journal of the Linnean Society **115**:505-521.

Pigliucci, M. 2005. Evolution of phenotypic plasticity: where are we going now? Trends in Ecology & Evolution **20**:481-486.

Pinchen, B. J. 2009. An update on the occurrences of various mole cricket species *Gryllotalpa* spp. in the British Isles since 2005. Atropos **36**:12-15.

Pocock, M. J., S. E. Newson, I. G. Henderson, J. Peyton, W. J. Sutherland, D. G. Noble, S. G. Ball, B. C. Beckmann, J. Biggs, and T. Brereton. 2015a. Developing and enhancing biodiversity monitoring programmes: a collaborative assessment of priorities. Journal of Applied Ecology **52**:686-695.

Pocock, M. J., H. E. Roy, C. D. Preston, and D. B. Roy. 2015b. The Biological Records Centre: a pioneer of citizen science. Biological Journal of the Linnean Society **115**:475-493.

Pocock, M. J., J. C. Tweddle, J. Savage, L. D. Robinson, and H. E. Roy. 2017. The diversity and evolution of ecological and environmental citizen science. PLoS One **12**:e0172579.

Pocock, M. J. O. 2011. Can traits predict species' vulnerability? A test with farmland passerines in two continents. Proceedings of the Royal Society B: Biological Sciences **278**:1532-1538.

Pocock, M. J. O., S. Hartley, M. G. Telfer, C. D. Preston, and W. E. Kunin. 2006. Ecological correlates of range structure in rare and scarce British plants. Journal of Ecology **94**:581-596.

Pollard, E. 1977. A method for assessing changes in the abundance of butterflies. Biological Conservation **12**:115-134.

Pollard, E. and T. Yates. 1992. The extinction and foundation of local butterfly populations in relation to population variability and other factors. Ecological Entomology **17**:249-254.

Pollard, E. and T. Yates. 1993. Monitoring Butterflies for Ecology and Conservation. Chapman & Hall, London.

Poniatowski, D. and T. Fartmann. 2009. Experimental evidence for density-determined wing dimorphism in two bush-crickets (Ensifera: Tettigoniidae). European Journal of Entomology **106**:599-605.

Poniatowski, D. and T. Fartmann. 2011a. Dispersal capability in a habitat specialist bush cricket: the role of population density and habitat moisture. Ecological Entomology **36**:717-723.

Poniatowski, D. and T. Fartmann. 2011b. Does wing dimorphism affect mobility in Metrioptera roeselii (Orthoptera: Tettigoniidae)? European Journal of Entomology **108**:409-415.

Poniatowski, D. and T. Fartmann. 2011c. Weather-driven changes in population density determine wing dimorphism in a bush-cricket species. Agriculture, Ecosystems & Environment **145**:5-9.

Poniatowski, D., S. Heinze, and T. Fartmann. 2012. The role of macropters during range expansion of a wing-dimorphic insect species. Evolutionary Ecology **26**:759-770.

Powney, G. D. and N. J. Isaac. 2015. Beyond maps: a review of the applications of biological records. Biological Journal of the Linnean Society **115**:532-542.

Powney, G. D., C. D. Preston, A. Purvis, W. van Landuyt, and D. B. Roy. 2014. Can trait-based analyses of changes in species distribution be transferred to new geographic areas? Global Ecology and Biogeography **23**:1009-1018.

Preston, C. 2013. Following the BSBI's lead: the influence of the *Atlas of the British flora*, 1962–2012. New Journal of Botany **3**:2-14.

Preston, C. D. and M. O. Hill. 1997. The geographical relationships of British and Irish vascular plants. Botanical Journal of the Linnean Society **124**:1-120.

Preston, C. D., D. Pearman, and T. D. Dines. 2002. New atlas of the British & Irish flora : an atlas of the vascular plants of Britain, Ireland, the Isle of Man and the Channel Islands. Oxford University Press, Oxford.

Preston, C. D., D. B. Roy, and H. E. Roy. 2012. What have we learnt from 50 years of biological recording? British Wildlife **24**:97-106.

Purse, B. V., R. Comont, A. Butler, P. M. Brown, C. Kessel, and H. E. Roy. 2015. Landscape and climate determine patterns of spread for all colour morphs of the alien ladybird *Harmonia axyridis*. Journal of Biogeography **42**:575-588.

Purse, B. V., S. J. Gregory, P. Harding, and H. E. Roy. 2012. Habitat use governs distribution patterns of saprophagous (litter-transforming) macroarthropods - a case study of British woodlice (Isopoda: Oniscidea). European Journal of Entomology **109**:543-552.

Pywell, R. F., M. S. Heard, B. A. Woodcock, S. Hinsley, L. Ridding, M. Nowakowski, and J. M. Bullock. 2015. Wildlife-friendly farming increases crop yield: evidence for ecological intensification. Proceedings of the Royal Society of London B: Biological Sciences **282**.

Quinn, G. P. and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team. 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ragge, D. R. 1965. Grasshoppers, Crickets and Cockroaches of the British Isles. Frederick Warne, London.

Ragge, D. R. and W. J. Reynolds. 1998. The songs of the grasshoppers and crickets of western Europe. The Natural History Museum / Harley Books, London & Great Horkesley.

Reinhardt, K., G. Köhler, S. Maas, and P. Detzel. 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. Ecography **28**:593-602.

Richards, O. W. and N. Waloff. 1954. Studies on the biology and population dynamics of British grasshoppers. Anti-Locust Bulletin **17**:1-186.

Riede, K., F. Nischk, C. Dietrich, C. Thiel, and F. Schwenker. 2006. Automated Annotation of Orthoptera Songs: First Results from Analysing the DORSA Sound Repository. Journal of Orthoptera Research **15**:105-113.

Robinson, E. L., E. Blyth, D. B. Clark, J. Finch, and A. C. Rudd. 2015. Climate, Hydrology and Ecology research Support System dataset (1961-2012) [CHESS]. http://thredds-prod.nerc-lancaster.ac.uk/thredds/CHESS.html

Robinson, R. A. and W. J. Sutherland. 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology **39**:157-176.

Roff, D. 1986. The evolution of wing dimorphism in insects. Evolution **40**:1009-1020.

Rogelj, J., M. den Elzen, N. Höhne, T. Fransen, H. Fekete, H. Winkler, R. Schaeffer, F. Sha, K. Riahi, and M. Meinshausen. 2016. Paris Agreement climate proposals need a boost to keep warming well below 2 °C. Nature **534**:631-639.

Roth, T., M. Plattner, and V. Amrhein. 2014. Plants, birds and butterflies: short-term responses of species communities to climate warming vary by taxon and with altitude. PLoS One **9**:e82490.

Rothamsted Insect Survey. 2017. Rothamsted Insect Survey. Retrieved 12/04/2017 from http://www.rothamsted.ac.uk/insect-survey/resources

Rothery, P. and D. B. Roy. 2001. Application of generalized additive models to butterfly transect count data. Journal of Applied Statistics **28**:897-909.

Roy, D. B., P. T. Harding, C. D. Preston, and H. E. Roy, editors. 2014. Celebrating 50 years of the Biological Records Centre. Centre for Ecology & Hydrology, Wallingford.

Roy, D. B., P. Rothery, and T. Brereton. 2005. The design of a systematic survey scheme to monitor butterflies in the United Kingdom. Studies on the ecology and conservation of butterflies in Europe **1**:102-105.

Roy, D. B., P. Rothery, and T. Brereton. 2007. Reduced-effort schemes for monitoring butterfly populations. Journal of Applied Ecology **44**:993-1000.

Roy, D. B., P. Rothery, D. Moss, E. Pollard, and J. Thomas. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. Journal of animal ecology **70**:201-217.

Roy, D. B. and T. H. Sparks. 2000. Phenology of British butterflies and climate change. Global Change Biology **6**:407-416.

Roy, H. E., T. Adriaens, N. J. B. Isaac, M. Kenis, T. Onkelinx, G. San Martin, P. M. J. Brown, L. Hautier, R. Poland, D. B. Roy, R. Comont, R. Eschen, R. Frost, R. Zindel, J. Van

Vlaenderen, O. Nedved, H. P. Ravn, J. C. Gregoire, J. C. de Biseau, and D. Maes. 2012. Invasive alien predator causes rapid declines of native European ladybirds. Diversity and Distributions **18**:717-725.

Royston, J. P. 1982. An extension of Shapiro and Wilk's *W* test for normality to large samples. Applied Statistics:115-124.

Rudkin, P. 2012. Pers. comm. to B. C. Beckmann, 15 July 2012.

Rybicki, J. and I. Hanski. 2013. Species–area relationships and extinctions caused by habitat loss and fragmentation. Ecology Letters **16**:27-38.

Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature **392**:491-494.

Schirmel, J., S. Buchholz, and T. Fartmann. 2010. Is pitfall trapping a valuable sampling method for grassland Orthoptera? Journal of Insect Conservation **14**:289-296.

Schouten, M. A., P. A. Verweij, A. Barendregt, R. J. M. Kleukers, and P. C. De Ruiter. 2007. Nested assemblages of Orthoptera species in the Netherlands: the importance of habitat features and life-history traits. Journal of Biogeography **34**:1938-1946.

Schweiger, O., J. Settele, O. Kudrna, S. Klotz, and I. Kühn. 2008. Climate change can cause spatial mismatch of trophically interacting species. Ecology **89**:3472-3479.

Seufert, V., N. Ramankutty, and J. A. Foley. 2012. Comparing the yields of organic and conventional agriculture. Nature **485**:229-232.

Shapiro, S. S. and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrika:591-611.

Shirt, D. B. 1987. British Red Data Books: 2. Insects. Nature Conservancy Council, Peterborough.

Silvertown, J. 2009. A new dawn for citizen science. Trends in Ecology & Evolution **24**:467-471.

Simberloff, D. 2009. The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and Systematics **40**:81-102.

Simmons, A. D. 2003. Changes in dispersal during range expansion. Ph.D. thesis. University of Leeds.

Simmons, A. D. 2015. Pers. comm. to B. C. Beckmann, 8 April 2015.

Simmons, A. D. and C. D. Thomas. 2004. Changes in Dispersal during Species' Range Expansions. American Naturalist **164**:378-395.

Skarpaas, O. and K. Shea. 2007. Dispersal patterns, dispersal mechanisms, and invasion wave speeds for invasive thistles. The American Naturalist **170**:421-430.

Skelton, M. 1974. Provisional atlas of the insects of the British Isles: Odonata and Orthoptera. Biological Records Centre, Institute of Terrestrial Ecology, Abbots Ripton, Huntingdon.

Skelton, M. J. 1978. Provisional Atlas of the Insects of the British lsles, Part 6, Orthoptera. Instititute of Terrestrial Ecology, Huntingdon.

Smith, G. 2007. Bush crickets on the menu. Essex Field Club Newsletter **54**:8-9.

Stanbury, A., F. Burns, M. Eaton, and J. Wilkinson. 2015. The National Amphibian and Reptile Recording Scheme (NARRS) Review - unpublished report.

Stevens, C. J., S. M. Smart, P. Henrys, L. Maskell, K. J. Walker, C. D. Preston, E. Crowe, D. Gowing, and B. Emmett. 2011. Collation of evidence of nitrogen impacts on vegetation in relation to UK biodiversity objectives. JNCC Report No. 447. Joint Nature Conservation Committee, Peterborough.

Stevens, V. M., C. Turlure, and M. Baguette. 2010. A meta-analysis of dispersal in butterflies. Biological Reviews **85**:625-642.

Suggitt, A. J., P. K. Gillingham, J. K. Hill, B. Huntley, W. E. Kunin, D. B. Roy, and C. D. Thomas. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. Oikos **120**:1-8.

Suggitt, A. J., C. Stefanescu, F. Páramo, T. Oliver, B. J. Anderson, J. K. Hill, D. B. Roy, T. Brereton, and C. D. Thomas. 2012. Habitat associations of species show consistent but weak responses to climate. Biology Letters **8**:590-593.

Sutherland, W. J. and D. A. Hill, editors. 1995. Managing habitats for conservation. Cambridge University Press, Cambridge.

Sutherland, W. J., A. S. Pullin, P. M. Dolman, and T. M. Knight. 2004. The need for evidence-based conservation. Trends in Ecology & Evolution **19**:305-308.

Sutton, P. 1999. The scaly cricket in Britain: a complete history from discovery to citizenship. British Wildlife **14**:145-151.

Sutton, P. G. 2007. Wildlife reports: grasshoppers and relatives. British Wildlife **18**:203-205.

Sutton, P. G. 2008. Wildlife reports: grasshoppers and relatives. British Wildlife **19**:432-433.

Sutton, P. G. 2015. A review of the Orthoptera (Grasshoppers and crickets) and allied species of Great Britain: Orthoptera, Dictyoptera, Dermaptera, Phasmida. Species Status No. 21. Natural England Commissioned Report NECR187.

Sutton, P. G., B. C. Beckmann, and B. Nelson. in press. The current status of orthopteroid insects in Britain and Ireland. Atropos.

Tack, A. J., T. Mononen, and I. Hanski. 2015. Increasing frequency of low summer precipitation synchronizes dynamics and compromises metapopulation stability in the Glanville fritillary butterfly. Proceedings of the Royal Society of London B: Biological Sciences **282**:20150173.

Telfer, M. G., C. D. Preston, and P. Rothery. 2002. A general method for measuring relative change in range size from biological atlas data. Biological Conservation **107**:99-109.

Thackeray, S. J., P. A. Henrys, D. Hemming, J. R. Bell, M. S. Botham, S. Burthe, P. Helaouet, D. G. Johns, I. D. Jones, D. I. Leech, E. B. Mackay, D. Massimino, S. Atkinson, P. J. Bacon, T. M. Brereton, L. Carvalho, T. H. Clutton-Brock, C. Duck, M. Edwards, J. M. Elliott, S. J. G. Hall, R. Harrington, J. W. Pearce-Higgins, T. T. Høye, L. E. B. Kruuk, J. M. Pemberton, T. H. Sparks, P. M. Thompson, I. White, I. J. Winfield, and S. Wanless. 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature **535**:241-245.

Thackeray, S. J., T. H. Sparks, M. Frederiksen, S. Burthe, P. J. Bacon, J. R. Bell, M. S. Botham, T. M. Brereton, P. W. Bright, L. Carvalho, T. Clutton-Brock, A. Dawson, M. Edwards, J. M. Elliott, R. Harrington, D. Johns, I. D. Jones, J. T. Jones, D. I. Leech, D. B. Roy, W. A. Scott, M. Smith, R. J. Smithers, I. J. Winfield, and S. Wanless. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology **16**:3304-3313.

Theobald, E., A. Ettinger, H. Burgess, L. DeBey, N. Schmidt, H. Froehlich, C. Wagner, J. HilleRisLambers, J. Tewksbury, and M. Harsch. 2015. Global change and local solutions: Tapping the unrealized potential of citizen science for biodiversity research. Biological Conservation **181**:236-244.

Thomas, C. and J. Abery. 1995. Estimating rates of butterfly decline from distribution maps: the effect of scale. Biological Conservation **73**:59-65.

Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conradt. 2001. Ecological and evolutionary processes at expanding range margins. Nature **411**:577-581.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004a. Extinction risk from climate change. Nature **427**:145-148.

Thomas, C. D., A. M. Franco, and J. K. Hill. 2006. Range retractions and extinction in the face of climate warming. Trends in Ecology & Evolution **21**:415-416.

Thomas, J., C. Thomas, D. Simcox, and R. Clarke. 1986. Ecology and declining status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain. Journal of Applied Ecology **23**:365-380.

Thomas, J. A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philosophical Transactions of the Royal Society B: Biological Sciences **360**:339.

Thomas, J. A. and R. T. Clarke. 2004. Extinction Rates and Butterflies. Science **305**:1563-1564.

Thomas, J. A., D. Simcox, and R. T. Clarke. 2009. Successful conservation of a threatened Maculinea butterfly. Science **325**:80-83.

Thomas, J. A., M. G. Telfer, D. B. Roy, C. D. Preston, J. J. D. Greenwood, J. Asher, R. Fox, R. T. Clarke, and J. H. Lawton. 2004b. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science **303**:1879-1881.

Thorsen, S. 2014. Time and Date. Retrieved 20/02/2014 from www.timeanddate.com

Travis, J. M. and C. Dytham. 2012. Dispersal and climate change: a review of theory. *in* J. Clobert, M. Baguette, T. G. Benton, and D. Bullock, editors. Dispersal Ecology and Evolution. Oxford University Press, Oxford.

Travis, J. M., K. Mustin, T. G. Benton, and C. Dytham. 2009. Accelerating invasion rates result from the evolution of density-dependent dispersal. Journal of Theoretical Biology **259**:151-158.

Travis, J. M. J. and C. Dytham. 2002. Dispersal evolution during invasions. Evolutionary Ecology Research **4**:1119-1129.

Tweddle, J. C., L. D. Robinson, M. Pocock, and H. E. Roy. 2012. Guide to citizen science: developing, implementing and evaluating citizen science to study biodiversity and the environment in the UK. 1906698376, NERC/Centre for Ecology & Hydrology, Wallingford.

Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecological Applications **13**:1790-1801.

UK Butterfly Monitoring Scheme. 2017. UK Butterfly Monitoring Scheme. Retrieved 12/04/2017 from http://www.ukbms.org/

UK Met Office. 2012. UK Climate Projections (UKCP09). Retrieved 30/05/2013 from www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09

UK Met Office. 2013. Four degree interactive map. Retrieved 27/02/2017 from http://www.metoffice.gov.uk/climate-guide/climate-change/impacts/four-degree-rise/map

UK Met Office. 2015. What is climate change? Retrieved 27/02/2017 from http://www.metoffice.gov.uk/climate-guide/climate-change

UKBMS. 2006. UK Butterfly Monitoring Scheme: Calculation of log collated indices http://www.ukbms.org/popup_texts/calculation.htm

UNEP. 2017. Stockholm Convention on Persistent Organic Pollutants. Retrieved 28/02/2017 from http://chm.pops.int/TheConvention/Overview/tabid/3351/Default.aspx

Uvarov, B. P. 1966. Grasshoppers and Locusts: A Handbook of General Acridology. Vol. 1, Anatomy, Physiology, Development, Phase Polymorphism, Introduction to Taxonomy. Cambridge University Press, Cambridge.

Uvarov, B. P. 1977. Grasshoppers and Locusts: A Handbook of General Acridology. Vol. 2. Cambridge University Press, Cambridge.

van Huis, A., J. van Itterbeeck, H. Klunder, E. Mertens, A. Halloran, G. Muir, and P. Vantomme. 2013. Edible insects: future prospects for food and feed security. FAO Forestry Paper 171. 9251075964, Food and Agriculture Organization of the United Nations, Rome.

van Strien, A. J., C. A. M. van Swaay, and T. Termaat. 2013. Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. Journal of Applied Ecology **50**:1450-1458.

van Swaay, C., A. van Strien, K. Aghababyan, S. Astrom, M. Botham, T. Brereton, P. Chambers, S. Collins, M. Domenech Ferre, R. Escobes, R. Feldmann, J. M. Fernández-García, B. Fontaine, S. Goloshchapova, A. Gracianteparaluceta, A. Harpke, J. Heliölä, G. Khanamirian, R. Julliard, E. Kühn, A. Lang, P. Leopold, J. Loos, D. Maes, X. Mestdagh, Y. Monasterio, M. L. Munguira, T. Murray, M. Musche, E. Õunap, L. B. Pettersson, S. Popoff, I. Prokofev, T. Roth, D. Roy, J. Settele, C. Stefanescu, G. Švitra, S. M. Teixeira, A. Tiitsaar, R. Verovnik, and M. S. Warren. 2015. The European Butterfly Indicator for Grassland Species 1990-2013, Report VS2015.009. De Vlinderstichting, Wageningen.

van Swaay, C. A., P. Nowicki, J. Settele, and A. J. van Strien. 2008. Butterfly monitoring in Europe: methods, applications and perspectives. Biodiversity and Conservation **17**:3455-3469.

Vickery, V. R. 1965. Factors governing the distribution and dispersal of the recently introduced grasshopper, *Metrioptera roeselii* (Hgb.) (Orthoptera: Ensifera). Annals of the Entomological Society of Quebec **10**:165-171.

Wagenmakers, E.-J. and S. Farrell. 2004. AIC model selection using Akaike weights. Psychonomic Bulletin & Review **11**:192-196.

Waldbauer, G. 2003. What good are bugs? Insects in the web of life. Harvard University Press, Cambridge, MA.

Walker, K., O. Pescott, F. Harris, C. Cheffings, H. New, N. Bunch, and D. Roy. 2015. Making plants count: a new National Plant Monitoring Scheme for the United Kingdom. British Wildlife **26**:243–250.

Wallis de Vries, M. F., W. Baxter, and A. J. Van Vliet. 2011. Beyond climate envelopes: effects of weather on regional population trends in butterflies. Oecologia **167**:559-571.

Wallisdevries, M. F. and C. A. Van Swaay. 2006. Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. Global Change Biology **12**:1620-1626.

Walters, R. J., M. Hassall, M. G. Telfer, G. M. Hewitt, and J. P. Palutikof. 2006. Modelling dispersal of a temperate insect in a changing climate. Proceedings of the Royal Society B - Biological Sciences **273**:2017-2023.

Warren, M. S., J. K. Hill, J. A. Thomas, J. Asher, R. Fox, B. Huntley, D. B. Roy, M. G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S. G. Willis, J. N. Greatorex-Davies, D. Moss, and C. D. Thomas. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature **414**:65-69.

Weisberg, S. 2013. Applied linear regression. 4th edition. Wiley, New York.

Whitehorn, P. R., S. O'Connor, F. L. Wackers, and D. Goulson. 2012. Neonicotinoid pesticide reduces bumble bee colony growth and queen production. Science **336**:351-352.

Whitman, D. W. 2008. The significance of body size in the Orthoptera: a review. Journal of Orthoptera Research **17**:117-134.

Williamson, M. 1996. Biological Invasions. Chapman & Hall, London.

Williamson, M. and K. J. Gaston. 1999. A simple transformation for sets of range sizes. Ecography **22**:674-680.

Willott, S. J. 1997. Thermoregulation in four species of British grasshoppers (Orthoptera: Acrididae). Functional Ecology **11**:705-713.

Willott, S. J. and M. Hassall. 1998. Life-history responses of British grasshoppers (Orthoptera: Acrididae) to temperature change. Functional Ecology **12**:232-241.

Wilson, R. J., D. Gutiérrez, J. Gutiérrez, D. Martínez, R. Agudo, and V. J. Monserrat. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. Ecology Letters **8**:1138-1146.

Wilson, R. J., D. Gutierrez, J. Gutierrez, and V. J. Monserrat. 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. Global Change Biology **13**:1873-1887.

Wilson, R. J., C. D. Thomas, R. Fox, D. B. Roy, and W. E. Kunin. 2004. Spatial patterns in species distributions reveal biodiversity change. Nature **432**:393-396.

Wissmann, J., H. Schielzeth, and T. Fartmann. 2009. Landscape-scale expansion of Roesel's bush-cricket *Metrioptera roeselii* at the north-western range limit in central Europe (Orthoptera: Tettigoniidae). Entomologia Generalis **31**:317-326.

Wolff, E., I. Fung, B. Hoskins, J. Mitchell, T. Palmer, B. Santer, J. Shepherd, K. Shine, S. Solomon, K. Trenberth, J. Walsh, and D. Wuebbles. 2014. Climate Change: Evidence & Causes. An overview from the Royal Society and the US National Academy of Sciences. National Academy of Sciences and Royal Society, Washington DC and London.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) **73**:3-36.

Woodcock, B. A., N. J. Isaac, J. M. Bullock, D. B. Roy, D. G. Garthwaite, A. Crowe, and R. F. Pywell. 2016. Impacts of neonicotinoid use on long-term population changes in wild bees in England. Nature Communications **7**:12459.

Yudelman, M., A. Ratta, and D. F. Nygaard. 1998. Pest management and food production: looking to the future. International Food Policy Research Institute, Washington DC.

Zeileis, A. and T. Hothorn. 2002. Diagnostic checking in regression relationships. R News **2**:7-10.

Zilli, D., O. Parson, G. V. Merrett, and A. Rogers. 2014. A hidden Markov model-based acoustic cicada detector for crowdsourced smartphone biodiversity monitoring. Journal of Artificial Intelligence Research **51**:805-827.